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Abstract.— Atlantic croaker, *Micropogonias undulatus*, collected from commercial catches in Chesapeake Bay and in Virginia and North Carolina coastal waters during 1988-1991 (n=1,967) were aged from transverse otolith sections. Ages 1–8 were recorded, but eight-year-old fish were rare. Marginal increment analysis showed that for ages 1–7, annuli are formed once a year during the period April–May. Otolith age readings were precise: >99% agreement within and between readers. Observed lengths-at-age were highly variable and growth rate decreased after the first year. Despite the high variability in sizes-at-age, observed lengths for ages 1–7 fit the von Bertalanffy growth model (r^2=0.99; n=753) well. No differences in growth were found between sexes. Total annual instantaneous mortality (Z) estimated from maximum age and from a catch curve of Chesapeake Bay commercial catches ranged from 0.55 to 0.63. Our results do not indicate the existence of a group of larger, older Atlantic croaker in Chesapeake Bay compared with more southern waters and suggest that the hypothesis of a basically different population dynamics pattern for this species north and south of Cape Hatteras, North Carolina, should be reevaluated.

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Age, growth, and mortality of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay region, with a discussion of apparent geographic changes in population dynamics*

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The Atlantic croaker, *Micropogonias undulatus* (Linnaeus), is one of the most abundant inshore demersal fishes along the Atlantic and Gulf of Mexico coasts of the United States (Joseph, 1972). Although recent commercial and recreational catches have come primarily from the South Atlantic Bight and the Gulf of Mexico, Atlantic croaker still support important fisheries along the Mid-Atlantic coast, especially from Maryland to North Carolina (Wilk, 1981). In Chesapeake Bay, they are caught by commercial and recreational fishermen during late spring and early fall migrations and, to a lesser extent, during the summer. In winter, Atlantic croaker leave the Bay to overwinter off the coast of Virginia and North Carolina, where they are caught by otter trawl and gillnet fisheries (Haven, 1959).

Little is known about age, growth, and mortality of Atlantic croaker in the Middle Atlantic and Chesapeake Bay regions. Studies based on length frequencies (Haven, 1957; Chao and Musick, 1977) require considerable subjective interpretation given the extended spawning period of Atlantic croaker (Morse, 1980; Warlen, 1982; Barbieri et al., unpubl. ms.) and the difficulty in distinguishing modal groups at older ages (White and Chittenden, 1977; Jearld, 1983). Although scale-ageing has also been used (Welsh and Breder, 1923; Wallace, 1940; Ross 1988), problems in applying this method to Atlantic croaker have been widely reported (Roithmayr, 1965; Joseph, 1972; Barger and Johnson, 1980; Barbieri, 1993).

In this study we provide information on age, growth, and mortality of Atlantic croaker in the Chesa-

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peake Bay region using a validated otolith-ageing method. We also evaluate the relationship between otolith size and fish size and age, and discuss the implications of using otoliths for ageing Atlantic croaker. Finally, based on current information on growth, and size and age compositions in Chesapeake Bay, we discuss the hypothesis of White and Chittenden (1977) and Ross (1988) regarding the existence of a basically different population dynamics pattern for Atlantic croaker north and south of Cape Hatteras, North Carolina.

Methods

Atlantic croaker were collected between June 1988 and June 1991 from commercial pound-net, haul-seine, and gillnet fisheries which operate from early spring to early fall in Chesapeake Bay. Local fish processing houses and seafood dealers were contacted weekly or fortnightly, and one 22.7-kg (50-lb) box of fish of each available market grade (small, medium, or large) was purchased. Although boxes of fish were not randomly selected, Chittenden (1989) found only minor among-box differences in Atlantic croaker length compositions in pound-net and haul-seine catches. Because nearly all variation in size compositions was captured by the within-box variation, box selection did not present a problem.

Since Atlantic croaker migrate from Chesapeake Bay in early fall to overwinter offshore (Haven, 1959), samples for the period November–March were obtained from commercial trawlers which operate in Virginia and North Carolina shelf waters. Young of the year (90–114 mm total length, TL) used to validate the first annulus on otoliths were obtained from the Virginia Institute of Marine Science juvenile bottom trawl survey.

Fish were measured for total length (TL, ±1.0 mm), weighed for total weight (TW, ±1.0 g), sexed, and both sagittal otoliths removed and stored dry. The left otolith was transversely sectioned through the core with the diamond blade of a Buehler low-speed Isomet saw. Sections 350–500 μm thick were mounted on glass slides with Flo-texx clear mounting medium and read under a dissecting microscope (6–12×) with transmitted light and bright field, with the exception of samples from the period April–May, when sections were also read with reflected light and dark field to help identify the last annulus.

Ages were assigned based on annulus counts; January 1 was taken as an arbitrary average birthdate when fish from one age class were assigned to the next oldest (Jearld, 1983). Although the average spawning date (average biological birthdate) of Atlantic croaker in the Chesapeake Bay region occurs in September (Barbieri et al., unpubl. ms.), we chose, for ageing purposes, to use January 1 as the average birthdate because annuli are formed during the period April–May (see Age determination below). To assess ageing precision, all otolith sections (n=1,967) were read twice by each of two readers, and agreement between readings and readers evaluated by percent agreement. All disagreements were resolved by a third reading with both readers.

Annuli were validated by the marginal increment method (Bagenal and Tesch, 1978). For each age, the translucent margin outside the proximal end of the last annulus was measured along the ventral side of the otolith sulcal groove (Fig. 1). Measurements (±0.02 mm) were taken with an ocular micrometer at 25×.

To evaluate growth, observed lengths at ages 1–7 were fit to the von Bertalanffy model (Ricker, 1975) by using nonlinear regression (Marquardt method). Model parameters were the following: L_∞, the mean asymptotic length; K, the Brody growth coefficient; and t_0, the hypothetical age at which a fish would have zero length (Ricker, 1975). To correct for growth after the time of annulus formation, only data for September, the peak spawning and thus average biological birthdate for Atlantic croaker in the Chesapeake Bay region (Barbieri et al., unpubl. ms.), were used for growth analysis.

To evaluate changes in otolith size relative to fish length and age, 30 randomly selected otoliths per age, for ages 1–7 (198–400 mm TL), were measured for maximum length (OL, ±0.05 mm) and maximum thickness (OT, ±0.05 mm), and weighed (OW, ± 0.001 g). After sectioning, otoliths were measured for otolith radius (OR, ±0.02 mm), defined as the distance between the center of the core and the otolith outer edge along the ventral side of the sulcal groove (Fig. 1). Relationships between otolith measurements and fish TL were evaluated by regression analysis. The effect of fish age on these relationships was evaluated by analysis of covariance (ANCOVA).

Linear regression was used to determine a length-weight relationship for fish ranging from 152 to 400 mm TL (36.3 to 967.0 g TW). Difference between sexes was tested by ANCOVA. The hypothesis of isometric growth (Ricker, 1975) was tested by t-test.

Instantaneous total annual mortality rates, Z, were estimated from maximum age by using Hoenig's pooled regression equation (Hoenig, 1983), by calculating a theoretical total mortality for the entire lifespan following the reasoning of Royce (1972), and by the regression method with a catch curve of combined pound-net, haul-seine, and gillnet

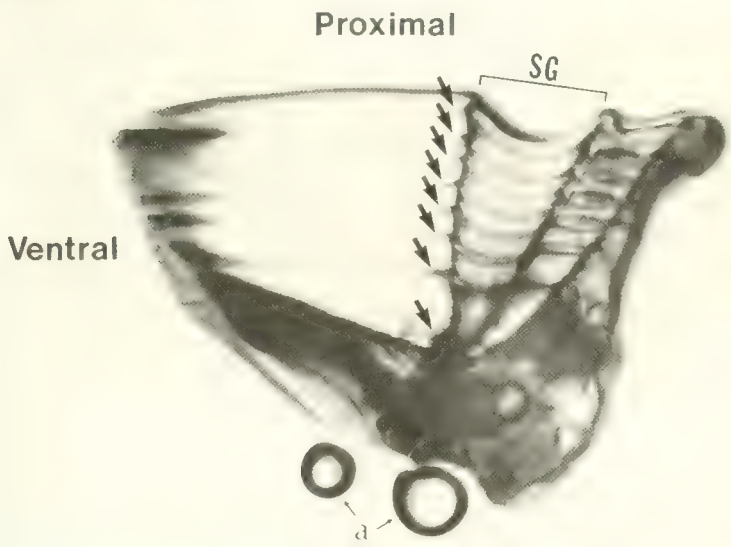

Figure 1

Transverse otolith section of an 8–year-old Atlantic croaker caught in September 1988 in Chesapeake Bay. Arrows indicate annuli. The translucent zone beyond the last annulus represents additional growth after the annulus was formed during April–May. SG =sulcal groove. a = artifact of preparation. Ventral and proximal indicate axes of orientation.

data for all recruited ages having five or more fish (Chapman and Robson, 1960). To avoid sampling bias associated with individual gears, we considered the age-frequency distribution obtained from data from combined gears as the best estimate of Atlantic croaker age composition in Chesapeake Bay (Ricker, 1975). Commercial trawl collections were not used in this analysis because they had different length compositions than the other gears and could be biased towards small fish. Because in catch curve analysis the age group represented by the apex of the catch curve may or may not be fully recruited to the gears (Everhart and Youngs, 1981), mortality estimates were based on ages 3–7 only. Data from 1988 to 1991 were combined to minimize the effect of variation in year-class strength (Robson and Chapman, 1961). The right tail of the catch curve (Ricker, 1975) was tested for deviation from linearity by analysis of variance (ANOVA). Values of Z were converted to total annual mortality rates, A, by using the relationship $A = 1 - e^{-Z}$ (Ricker, 1975).

All statistical analyses were performed by using the Statistical Analysis System (SAS, 1988). Rejection of the null hypothesis in statistical tests was based on α=0.05. F-tests in ANCOVA were based on Type III sums of squares (Freund and Littell, 1986). Assumptions of linear models were checked by residual plots as described in Draper and Smith (1981). For the OL-TL, OW-TL, and TW-TL relationships, and for all ANCOVA and ANOVA analyses, data were $\log_{10}$–transformed to correct for non-linearity and heterogeneous variances. For the catch curve analysis, $\log_e$-transformed numbers at age were regressed on age. Unless otherwise indicated, back-transformed data and regression equations are presented in the results.

Results

Age determination

Transverse otolith sections of Atlantic croaker show very clear, easily identified marks that can be used for ageing. Typical sections have an opaque core surrounded by a blurred opaque band composed of fine opaque and translucent zones (Fig. 1). This band represents the first annulus. The width of this annulus varies among fish, from a very narrow band that is almost continuous with the core, to a wide, well-defined band clearly separated from the core. Because of this variation in width and proximity to

the core, the first annulus is sometimes difficult to identify. Subsequent annuli are represented by easily identified, narrow, opaque bands that alternate with wider translucent bands outside the proximal margin of the first annulus (Fig. 1).

Annuli are formed on otoliths once a year in the period April–May. For ages 1–7, mean monthly marginal increment plots show only one minima during the year, indicating that only one annulus is formed each year (Fig. 2). The trough starts abruptly in April, a period when there is, in general, maximum variation in the mean marginal increment, suggesting that some fish have begun to form the annulus while others have not. Lowest marginal increment values occurred in May, the most intensive period of annulus formation. Marginal incre-

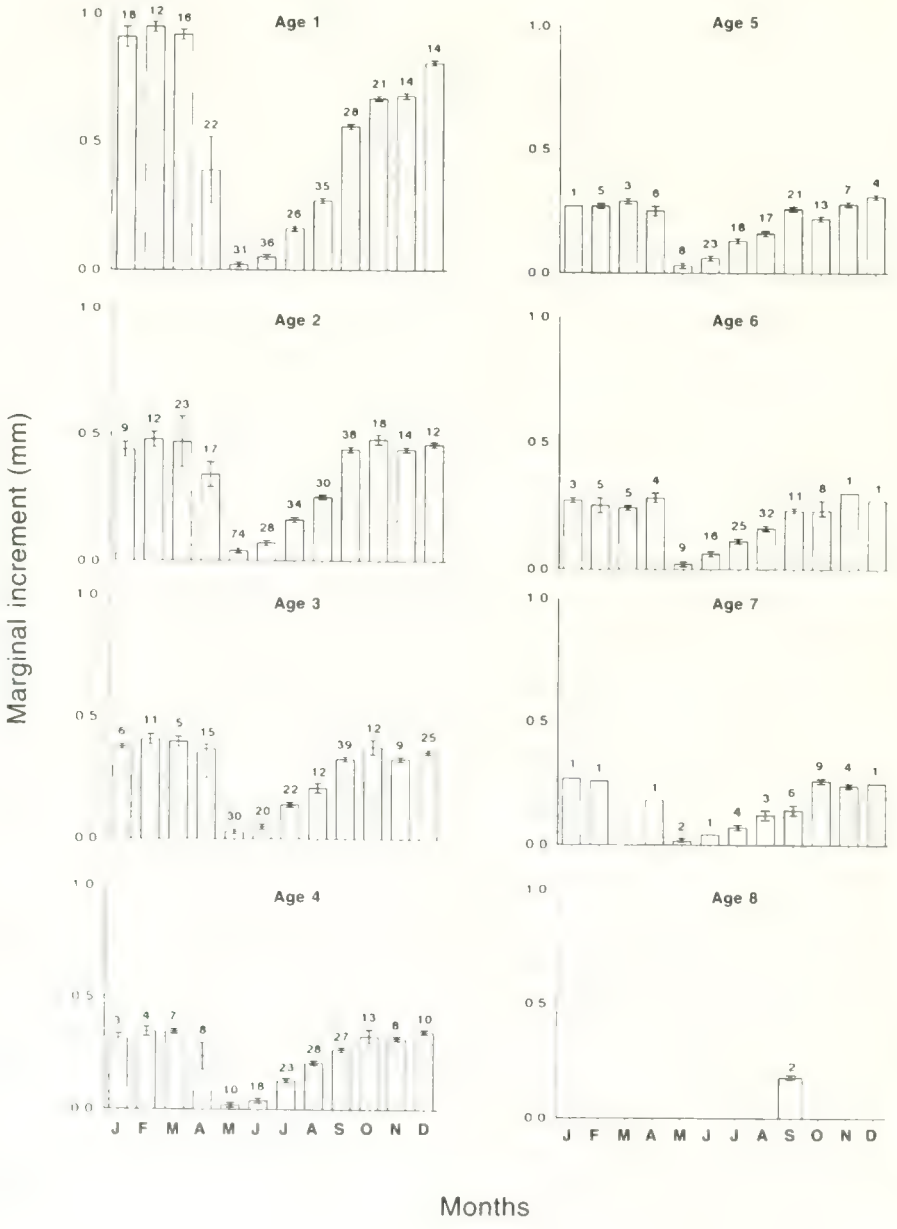

Figure 2

Mean monthly marginal increment for Atlantic croaker ages 1–8 from the Chesapeake Bay region, 1988–91. Vertical bars are ±1 standard error. Numbers above the bars are sample sizes.

ment values progressively rise to a somewhat stable maximum from October through March or April, indicating a period of little or no otolith growth. Because only two age-8 fish were collected, it was not possible to validate annuli beyond age 7.

To confirm our interpretation that the blurred opaque band around the otolith core represents the first annulus, (i.e., that fish hatched in the fall form a mark during their first spring), otolith sections of young of the year (94–114 mm) collected during the period March–June were examined. All those collected in March–April were developing fine opaque marks around the core, and all those in May–June had an opaque mark already formed (Fig. 3).

Otolith age readings were very precise, both within and between readers. Percent agreement was 99.5% for reader 1, 99.3% for reader 2, and 99.2% between readers. In all cases of disagreement, the difference never exceeded 1 year. Only one of the 1,967 left otoliths sectioned was crystallized and could not be read. In that case, the right otolith was read. Difficulty in ageing Atlantic croaker from otolith sections did not increase with increasing age. However, proper identification of the first annulus was very important. All disagreements, independent of age, were due to problems in identifying the first annulus.

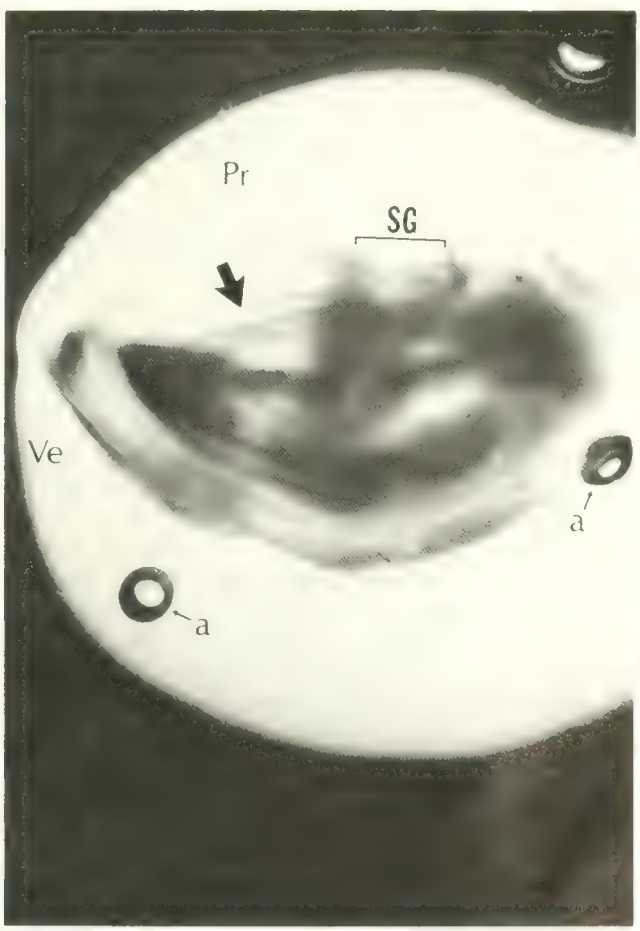

Figure 3

Transverse otolith section of a young-of-the-year Atlantic croaker (114 mm TL) collected in June 1990 in Chesapeake Bay. The arrow indicates the outer edge of the first annulus formed during the period April–May. SG=sulcal groove; Ve=ventral; Pr=proximal; a=artifact of preparation.

Otolith size relative to fish size and age

Changes in otolith size relative to fish size were not constant along all axes (Fig. 4). Otolith maximum length was the only axis that showed a linear, isometric increase with fish length. Otolith radius, the axis along which annuli were read in transverse sections, showed a non-linear relationship with fish length, and had the smallest r^2 of all variables (Fig. 4). The curvilinear relationship suggests that otolith growth relative to fish growth slows down along this axis as fish get bigger.

Despite its poor relationship with fish length, otolith radius showed a very strong linear relationship with fish age. An ANCOVA model showing length, age, and their interaction explained 97% of the variation in otolith radius (Table 1). All factors in the model were highly significant ($P<0.01$). Similar models for otolith maximum length, maximum thickness, and weight were also highly significant and had high coefficients of determination ($r^2 \geq 0.85$). However, significance for these models was due to fish length only, neither age nor the interaction factor was significant.

Growth

Observed lengths varied greatly within ages (Fig. 5). Atlantic croaker showed a rapid increase in size during the first year, but annual growth rate greatly decreased during the second year, remaining comparatively low thereafter (Fig. 5). On average, 64% of the cumulative total observed growth in length occurred in the first year and 84% was completed after two years.

No differences in mean lengths at age were found between sexes (t-test at each age; $P>0.05$ for all ages). Mean observed total lengths for pooled sexes were 201, 263, 274, 285, 290, 307, 309, and 313 mm, for ages 1–8, respectively.

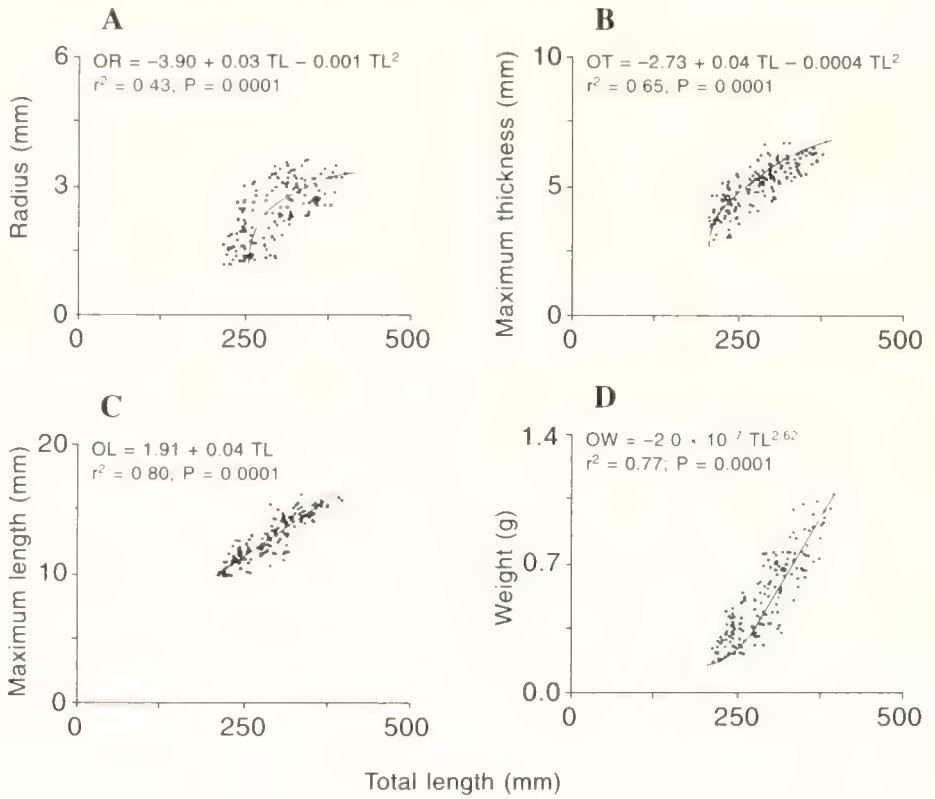

Figure 4

Scatter plots and fitted regression lines of different otolith measurements versus Atlantic croaker total length: (**A**) otolith radius (OR); (**B**) otolith maximum thickness (OT); (**C**) otolith maximum length (OL); and (**D**) otolith weight (OW). Sample size in each plot is 210.

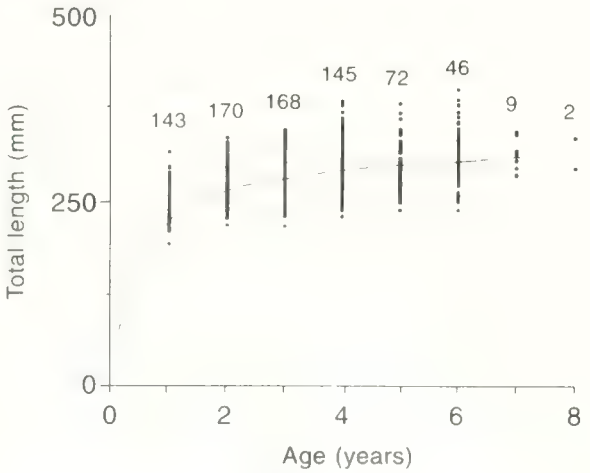

Figure 5

Observed lengths at age and fitted von Bertalanffy regression line for Atlantic croaker from the Chesapeake Bay region (September, 1988–91). Numbers above data points are sample sizes at each age.

Despite the high variability in sizes at age, observed lengths at ages 1–7 showed a very good fit to the von Bertalanffy growth model (r^2=0.99; n=753). Estimated model parameters, asymptotic standard errors, and 95% confidence intervals are given in Table 2.

No difference in the length-weight relationship was found between sexes (ANCOVA; F=2.46; df=3,005; P=0.15). The equation for pooled sexes (Fig. 6) was

$$TW = 2.41\times10^{-6}TL^{3.30}\ (r^2 = 0.97; n = 3{,}006; P < 0.01).$$

The slope of the regression line (b=3.30; SE=0.0141) was significantly different from 3.00 (t-test; t=7.26; P<0.01), indicating allometric growth.

Size and age compositions

Length-frequency distributions of Atlantic croaker samples obtained from different fishing gears were similar (Fig. 7), with the exception of commercial trawl data which were dominated by fish smaller than 275 mm. The smallest Atlantic croaker cap-

Table 1

Summary of ANCOVA to evaluate the effect of Atlantic croaker (*Micropogonias undulatus*) total length (TL) and age on otolith maximum thickness (OT), maximum length (OL), weight (OW), and radius (OR). n = 210 for each analysis; α = 0.05.

Otolith relation	Source of variation	r^2	P-value
OT	model	0.85	0.0001
	TL		0.0001
	age		0.3263
	TL × age		0.6214
OL	model	0.88	0.0001
	TL		0.0001
	age		0.9780
	TL × age		0.7907
OW	model	0.90	0.0001
	TL		0.0001
	age		0.0863
	TL × age		0.1402
OR	model	0.97	0.0001
	TL		0.0001
	age		0.0001
	TL × age		0.0008

tured by each gear was approximately 200 mm, although these data represent only market foodfish grades (small, medium, or large) and did not include smaller fish sold as scrap. The maximum length recorded was 400 mm, from a pound-net catch in 1988. However, for all gears 99% of the Atlantic croaker collected were ≤345 mm.

Age compositions from different gears were not as similar as length frequencies suggest (Fig. 7). Haul-seines, gill nets, and commercial trawls caught a large proportion of fish at ages 1 and 2, and had age 2 as the first age fully recruited. Pound nets captured a comparatively larger proportion of fish at ages 4–7, and had age 3 as the first age fully recruited. Age-1 fish were not fully recruited to any of the gears sampled, but this may reflect, in part, the exclusion of scrap fish from our collections.

The maximum age sampled was 8 years. Despite the large sample size and the variety of gears used, only two eight-year-old fish were collected, one from a pound net in September 1988 (334 mm) and one from a gill net in September 1990 (293 mm).

Mortality

Instantaneous total annual mortality rates (Z) ranged from 0.55 to 0.63. Estimates obtained for a maximum age of 8 years were 0.55 (A=42%) by using Hoenig's (1983) method, and 0.58 (A=43%) by using Royce's (1972) method. A regression estimate obtained from the slope of the catch curve (Fig. 8) was 0.63 (A=47%); confidence intervals were 0.36 (A=30%) and 0.90 (A=59%). The regression line did not deviate significantly from linearity (ANOVA; F=1.15; P=0.40).

Table 2

Parameter estimates, standard errors, and 95% confidence intervals for the von Bertalanffy growth model for Atlantic croaker (*Micropogonias unpulatus*) in the Chesapeake Bay region (1988–90).

Parameter	Estimate	Standard error	95% confidence intervals	
			Lower	Upper
L_∞	312.43	7.44	297.82	327.04
K	0.36	0.08	0.20	0.52
t_0	−3.26	0.84	−4.91	−1.61

Discussion

Age determination

Our criteria for ageing Atlantic croaker from otolith sections differ from those of Barger (1985), in that we considered the first annulus to be the blurred opaque band surrounding the otolith core. However, evidence from both studies seems to support our interpretation. Barger (1985) reported 58% of the otoliths in his samples had marks that were too thin or discontinuous and too close to the core to be considered annuli. By examining otoliths of young of the year during the period of annulus formation, we were able to validate this mark as the first annulus, formed during their first spring in the estuary. Because spawning of Atlantic croaker in the Chesapeake Bay area extends from late July to December (Barbieri et al., unpubl. ms.) and the first annulus is formed during their first spring after hatching, fish forming the first annulus could range from 5 to 10 months of age. As marginal increment plots indicated, all subsequent annuli formed at yearly intervals.

Variation in the width of the first annulus also seems to reflect the protracted spawning period of Atlantic croaker. Early hatched fish (July–August) would probably be large enough by April or May to have this annulus close to, but not continuous with, the otolith core. In contrast, late-hatched fish (November–December) would be small in the spring and

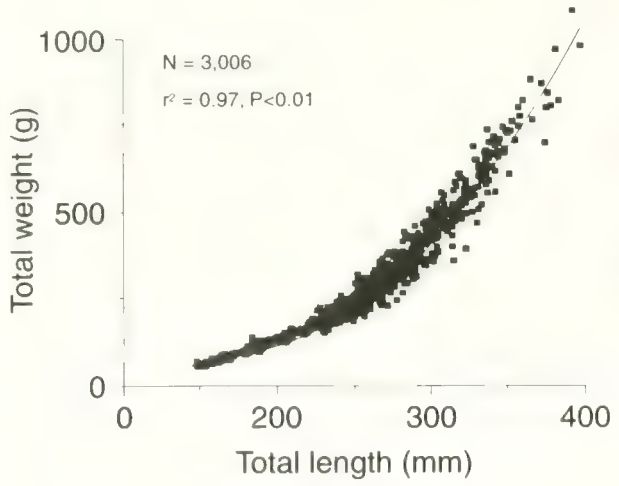

Figure 6
Length-weight relationship of Atlantic croaker in the Chesapeake Bay region, 1988–91.

would probably show the first mark and the core virtually fused together. Since Atlantic croaker also spawn over a long period in the Gulf of Mexico (White and Chittenden, 1977), this might explain why the first annulus was apparent in only a portion of Barger's (1985) fish.

Our interpretation of the first annulus is also consistent with evidence from another ageing method. Ross (1988) reported that some Atlantic croaker from North Carolina showed an early, age-0 scale mark, apparently formed during their first winter. However, they were not counted as annuli.

The high precision of repeated age readings and validation of annuli almost to the maximum observed age indicate that otolith sections represent a very reliable method for ageing Atlantic croaker. Identifying the first annulus may require some practice, but all other annuli are extremely clear and easy to identify. Otolith sections do not have the problems scales reportedly do, such as the occurrence of double marks (White and Chittenden, 1977; Music and Pafford, 1984; Ross, 1988; Barbieri, 1993), or marks that are poorly defined and difficult to distinguish (Joseph, 1972; Barger and Johnson, 1980; Barbieri, 1993).

The pattern of otolith growth relative to fish growth also indicated the high reliability of transverse otolith sections for ageing Atlantic croaker. Although otolith radius, the axis we used to read annuli, showed a poor correlation with fish length, the strong linear relationship between otolith radius and age indicates that otolith growth along this axis seems to be continuous with age, independent of fish growth. This supports previous suggestions (Mosegaard et al., 1988; Wright, 1991) that a process other than somatic growth governs the rate of otolith accretion. Because otoliths grow at a faster rate than the body during slow somatic growth, they are excellent structures for recording the seasonal cycle and age in slow-growing and old fish, especially those approaching asymptotic length (Casselman, 1990). The high correlation we found between otolith radius and age for Atlantic croaker seems to confirm this pattern.

Growth and mortality

High variability of observed lengths at age indicates that length is a very poor predictor of age for Atlantic croaker, especially beyond age 2. The wide range in lengths at age can be attributed to a combination of two factors: 1) most of Atlantic croaker's growth occurs during the first two years, becoming asymptotic after age 2; and 2) fish are born at different times during the extended spawning season and display different growth rates. Warlen (1982) reported that Atlantic croaker larvae caught later in the spawning season had slower growth rates than those taken during peak spawning. Since growth decreases sharply after their first year, such differences in growth rates among young of the year is likely to cause a large variation in lengths at age.

Growth parameter estimates reported here do not agree with previous reports for Atlantic croaker. However, comparisons with previous studies are difficult because other estimates were based on different ageing methods (White and Chittenden, 1977; Ross, 1988), different otolith-ageing criteria (Barger, 1985; Hales and Reitz, 1992), or a period before any significant fishery for Atlantic croaker occurred (Hales and Reitz, 1992). Methods used to estimate length-at-age data or to fit the von Bertalanffy model also varied. Previous studies on Atlantic croaker growth generally used back-calculated rather than observed lengths at age. Although back-calculation has been widely used and represents standard methodology in age and growth studies (Bagenal and Tesch, 1978; Jearld, 1983), recent evidence indicates that it may generate biased results (Campana, 1990; Ricker, 1992). By basing our growth parameter estimates on observed lengths at age of fish collected in September—the average spawning period of Atlantic croaker in the Chesapeake Bay area—we avoided problems related to back-calculation procedures or seasonal growth effects.

Our total mortality estimates are the lowest ever

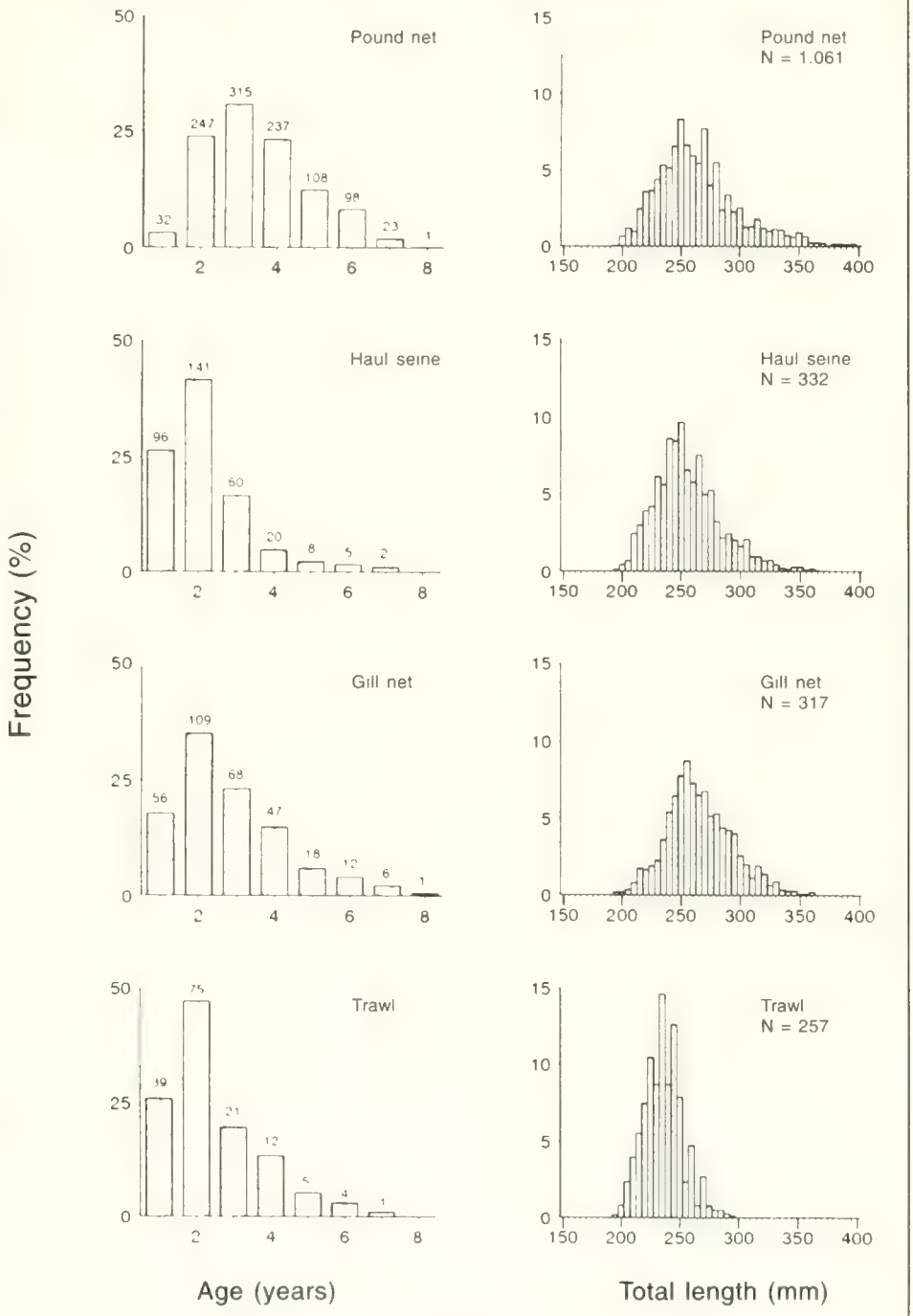

Figure 7

Age frequency (left panels) and length frequency (right panels) distributions by fishing gear for Atlantic croaker in the Chesapeake Bay region, 1988–91. Numbers above bars are sample sizes by age.

reported for Atlantic croaker. However, the close agreement we found between estimates obtained from maximum age and from the catch curve indicates our values are probably realistic, at least for the Chesapeake Bay area. Comparisons with previous studies are difficult because other estimates were based on different ageing methods (scales and length frequencies), and on collections from a single sampling gear and different geographical areas (White and Chittenden, 1977; Ross, 1988).

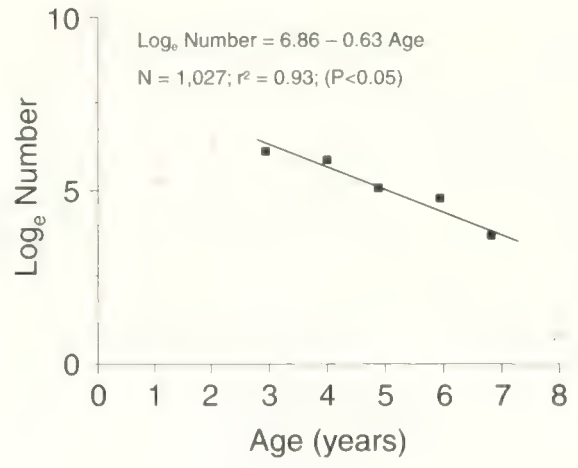

Figure 8

Catch curve for Atlantic croaker collected from pound-net, haul-seine and gillnet commercial catches in Chesapeake Bay, 1988–91. Ages 1, 2, and 8 (triangles) were not used in calculating the regression line.

Geographic comparisons

The possible existence of two groups of Atlantic croaker, exhibiting different life history and population dynamics attributes north and south of Cape Hatteras, North Carolina, has been extensively discussed in the scientific literature (Chittenden, 1977; White and Chittenden, 1977; Ross, 1988). Ross (1988) hypothesized that these groups may overlap and mix in North Carolina and stated that, if the Atlantic croaker designated in his study as "northern" were fish migrating south from the Chesapeake and Delaware Bay areas, their larger sizes (350–520 mm TL) and older ages (5–7 years, as aged by scales) would be consistent with the proposed northern group life history pattern. However, our results do not support the hypothesis of a group of larger, older Atlantic croaker in Chesapeake Bay, at least in recent years.

Maximum length and size ranges reported here are consistent with recent data from North Carolina, both for inshore waters as well as for the offshore trawl fishery. Since 1982, Atlantic croaker trawl catches in North Carolina have been dominated by small fish. Fish larger than 300 mm TL and older than 3 years have represented less than 1% of the recent catches (Ross, 1991). Although records of large fish do exist, Atlantic croaker as large as those reported by Ross (1988) have never been common in commercial catches from the Chesapeake Bay region. Even in the early 1930's, when the winter trawl fishery had just been established off the coasts of Virginia and North Carolina and catches of Atlantic croaker were dominated by large fish, most fish measured 260–360 mm TL (Pearson, 1932). Length frequencies of Atlantic croaker sampled from commercial pound nets in the lower Chesapeake Bay in 1922 (Hildebrand and Schroeder, 1928) and during 1950–1958 (Massmann and Pacheco, 1960), as well as from pound nets and haul-seines in Pamlico and Core sounds, North Carolina (Higgins and Pearson, 1928), show the same pattern.

Recreational catch records also indicate that the large Atlantic croaker reported by Ross (1988) have not been common in the Chesapeake and Delaware Bay areas. Between 1960 and 1970 the minimum citation weight for Atlantic croaker in the Virginia Saltwater Fishing Tournament ranged from 0.91 to 1.36 kg. Although 741 citations were issued during this period, only 1.9% were for Atlantic croaker ≥1.82 kg. Between 1977 and 1982, however, although the minimum citation weight was raised to 1.82 kg, 599 citations were issued, including 47 entries for Atlantic croaker ≥2.27 kg (483–610 mm TL). The largest number of citations occurred in 1979 and 1980, coinciding with Ross's (1988) sampling period in North Carolina. Records from the Delaware State Fishing Tournament show the same pattern as that from Virginia. The number of citations was very small during the early 1970's, reached a peak in 1980, and decreased rapidly thereafter. Although complete information covering their entire range is not available, state records of Atlantic croaker along the east coast of the United States show the same pattern. Records from Georgia to New Jersey were broken during the period 1977–82, indicating that 1) unusually large fish occurred during this period and have not occurred since; and 2) their occurrence was not limited to areas north of North Carolina.

In conclusion, recent size and age composition data do not indicate the existence of a group of larger, older Atlantic croaker in the Chesapeake Bay region compared with more southern waters. Historic information agrees well with our results and indicates that fish >400 mm TL have not represented a large proportion of Atlantic croaker in this area. The abundance of unusually large fish during the period 1977–82 apparently constituted an unusual event and may reflect passage through the fishery of a few strong year classes that seemingly disappeared after 1982. Similar episodes—the occurrence of larger fish for a few years—have been previously reported for Atlantic croaker in Chesapeake Bay (Hildebrand and Schroeder, 1928; Massmann and Pacheco, 1960), suggesting the phenomenon happens periodically. An increase in survivorship of

early spawned fish, combined with higher mortality of late-spawned fish as a result of low winter temperatures in estuarine nursery areas (Massmann and Pacheco, 1960; Joseph, 1972; Warlen and Burke, 1991) could account for an increase in the proportion of larger fish in certain years and explain the episodic occurrence of large Atlantic croaker in this area.

Our results for Chesapeake Bay, together with records of large fish south of North Carolina during 1977–82, suggest that the hypothesis of a basically different life history and population dynamics pattern for Atlantic croaker north and south of Cape Hatteras, North Carolina, should be reevaluated. However, sampling programs over time describing size and age compositions of Atlantic croaker throughout their range are still necessary to fully evaluate this question.

Acknowledgments

We would like to thank the Chesapeake Bay commercial fishermen and James Owens (VIMS) for helping us obtain samples. Sue Lowerre-Barbieri helped with fish processing and with otolith sectioning and reading. Claude Bain (Virginia Saltwater Fishing Tournament) and Jessie Anglin (Delaware Department of Natural Resources) provided information on Atlantic croaker recreational citation records. Ronald Hardy, Joe Loesch, Sue Lowerre-Barbieri, Jack Musick, Rogerio Teixeira, and two anonymous reviewers made helpful suggestions to improve the manuscript. Financial support was provided by the College of William and Mary, Virginia Institute of Marine Science, by Old Dominion University, Applied Marine Research Laboratory, and by a Wallop/Breaux Program Grant for Sport Fish Restoration from the U.S. Fish and Wildlife Service through the Virginia Marine Resources Commission, Project No. F-88–R3. Luiz R. Barbieri was partially supported by a scholarship from CNPq, Ministry of Science and Technology, Brazil (process No. 203581/86–OC).

Literature cited

Bagenal, T. B., and F. W. Tesch.
1978. Age and growth. *In* T. B. Bagenal (ed.), Methods for assessment of fish production in fresh waters, 3rd ed., p. 101–136. Blackwell Scientific Publications, Oxford.

Barbieri, L. R.
1993. Life history, population dynamics, and yield-per-recruit modeling of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay area. Ph.D. diss., School of Marine Science, College of William and Mary, VA, 140 p.

Barger, L. E.
1985. Age and growth of Atlantic croakers in the northern Gulf of Mexico, based on otolith sections. Trans. Am. Fish. Soc. 114:847–850.

Barger, L. E., and A. G. Johnson.
1980. An evaluation of marks on hardparts for age determination of Atlantic croaker, spot, sand seatrout, and silver seatrout. NOAA Tech. Memo, NMFS, SEFC-22.

Campana, S. E.
1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. 47:2219–2227.

Casselman, J. M.
1990. Growth and relative size of calcified structures of fish. Trans. Am. Fish. Soc. 119:673–688.

Chao, L. N., and J. A. Musick.
1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull. 75:657–702.

Chapman, D. G., and D. S. Robson.
1960. The analysis of a catch curve. Biometrics 16:354–368.

Chittenden, M. E., Jr.
1977. Simulations of the effects of fishing on the Atlantic croaker, *Micropogon undulatus*. Proc. Gulf Carib. Fish. Inst. 29:68–86.
1989. Sources of variation in Chesapeake Bay pound-net and haul-seine catch compositions. N. Am. J. Fish. Mgmt. 5:86–90.

Draper, N. R., and H. Smith.
1981. Applied regression analysis, 2nd ed. John Wiley & Sons, NY, 709 p.

Everhart, W. H., and W. D. Youngs.
1981. Principles of fishery science, 2nd ed. Cornell University Press, Ithaca, 349 p.

Freund, R. J., and R. Littell.
1986. SAS system for linear models, 1986 ed. SAS Institute Incorporated, Cary, NC.

Hales, L. S., Jr., and E. J. Reitz.
1992. Historical changes in age and growth of Atlantic croaker, *Micropogonias undulatus* (Perciformes: Sciaenidae). J. Archaeol. Sci. 19:73–99.

Haven, D. S.
1957. Distribution, growth, and availability of juvenile croaker, *Micropogon undulatus*, in Virginia. Ecology 38:88–97.
1959. Migration of the croaker, *Micropogon undulatus*. Copeia 1959:25–30.

Higgins, E., and J. C. Pearson.
1928. Examination of the summer fisheries of Pamlico and Core sounds, N.C., with special reference to the destruction of undersized fish and the protection of the gray trout, *Cynoscion regalis*. Rep. U.S. Comm. Fish. 2:29–65.

Hildebrand, S. F., and W. C. Schroeder.
1928. The fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43:1–388.

Hoenig, J. M.
1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82:898–902.

Jearld, A., Jr.
1983. Age determination. *In* L. A. Nielsen and D. L. Johnson (eds.), Fisheries techniques, p. 301–324. Am. Fish. Soc., Bethesda, MD.

Joseph, E. B.
1972. The status of the sciaenid stocks of the middle Atlantic coast. Chesapeake Sci. 13:87–100.

Massmann, W. H., and A. L. Pacheco.
1960. Disappearance of young Atlantic croakers from the York River, Virginia. Trans. Am. Fish. Soc., 89:154–159.

Morse, W. W.
1980. Maturity, spawning and fecundity of Atlantic croaker, *Micropogonias undulatus,* occurring north of Cape Hatteras, North Carolina. Fish. Bull. 78:190–195.

Mosegaard, H., H. Svendang, and K. Taberman.
1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. 45:1514–1524.

Music, J. L., Jr., and J. M. Pafford.
1984. Population dynamics and life history aspects of major marine sportfishes in Georgia's coastal waters. Georgia Dep. Nat. Res., Coast. Res. Div., Contr. Ser. No. 38, Brunswick, 382 p.

Pearson, J. C.
1932. Winter trawl fishery off the Virginia and North Carolina coasts. U.S. Bur. Fish., Invest. Rep. No. 10, Washington, 31 p.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.
1992. Back-calculation of fish lengths based on proportionality between scale and length increments. Can. J. Fish. Aquat. Sci. 49:1018–1026.

Robson, D. S., and D. G. Chapman.
1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181–189.

Roithmayr, C. M.
1965. Review of industrial bottomfish fishery in northern Gulf of Mexico, 1959–62. Comm. Fish. Rev., U.S. 27:1–6.

Ross, J. L.
1991. Assessment of the North Carolina winter trawl fishery, September 1985–April 1988. North Carolina Dep. Environ. Health Nat. Res., Div. Mar. Fish., Spec. Sci. Rep. No. 54, 80 p.

Ross, S. W.
1988. Age, growth, and mortality of Atlantic croaker in North Carolina, with comments on population dynamics. Trans. Am. Fish. Soc. 117:461–473.

Royce, W. F.
1972. Introduction to the fisheries sciences. Academic Press, NY, 351 p.

SAS. 1988.
SAS/STAT user's guide. Release 6.03 edition. SAS Institute Inc., Cary, NC, 1028 p.

Wallace, D. H.
1940. Sexual development of the croaker, *Micropogon undulatus*, and distribution of the early stages in Chesapeake Bay. Trans. Am. Fish. Soc. 70:475–482.

Warlen, S. M.
1982. Age and growth of larvae and spawning time of Atlantic croaker in North Carolina. Proc. Ann. Conf. S.E. Assoc. Fish and Wildl. Agencies 34:204–214.

Warlen, S. M., and J. S. Burke.
1991. Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. Estuaries 13:453–461.

Welsh, W. W., and C. M. Breder.
1923. Contributions to the life histories of Sciaenidae of the eastern United States coast. Bull. U.S. Bur. Fish. 39:141–201.

White, M. L., and M. E. Chittenden Jr.
1977. Age determination, reproduction, and population dynamics of the Atlantic croaker, *Micropogonias undulatus*. Fish. Bull. 75:109–123.

Wilk, S. J.
1981. The fisheries for Atlantic croaker, spot, and weakfish. *In* H. Clepper (ed.) Proceedings of the 6th annual marine recreational fisheries symposium, p. 5–27. Sport Fish. Inst., Washington.

Wright, P. J.
1991. The influence of metabolic rate on otolith increment width in Atlantic salmon parr, *Salmo salar* L. J. Fish Biol. 38:929–933.

Abstract.— Statolith microstructural analysis was applied to 126 specimens of the oceanic boreal clubhook squid, *Onychoteuthis borealijaponica*, for estimation of age and growth rates. Specimens were captured from the western, central, and eastern North Pacific between approximately lat. 38° N and 47°N by driftnet fishing, trawling, and jigging in the summers of 1990 and 1991. Results suggest that increments were deposited at a rate of one per day. Both sexes live approximately one year; males mature at smaller sizes and younger ages than females. Exponential growth models suggest that growth in length was similar for males and females (0.80% ML/day) in the central North Pacific, while growth in weight was higher for females (1.90% WT/day) than males (1.40% WT/day). Females in the western North Pacific exhibited faster growth rates than individuals from the central North Pacific. *O. borealijaponica* were estimated to have hatched year round based on back calculation of statolith increments from the time of capture. Post-recruit individuals exploited in the *O. borealijaponica* jig fishery and *Ommastrephes bartramii* driftnet fishery typically hatched from late summer to early winter.

Age and growth of the oceanic squid *Onychoteuthis borealijaponica* in the North Pacific

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The oceanic boreal clubhook squid *Onychoteuthis borealijaponica* Okada, 1927 is common in subarctic waters of the North Pacific. This species ranges from the western coast of the United States and Canada to the eastern coast of Hokkaido, Japan, and the Kurile Islands, but does not occur in the Sea of Okhotsk or Bering Sea (Young, 1972; Murata et al., 1976; Naito et al., 1977a; Fiscus and Mercer, 1982; and Kubodera et al., 1983). *Onychoteuthis borealijaponica* has commercial value throughout its range. Between 1971 and 1979, commercial landings averaged 1,171 metric tons (t) per year from a jig fishery in oceanic waters east of Hokkaido, Japan (Okutani and Murata, 1983), and approximately 254 and 2,705 t of *O. borealijaponica* were caught in 1990 and 1991, respectively, by Japan, Korea, and Taiwan in the *Ommastrephes bartramii* highseas driftnet fishery (DiNardo and Kwok, in review[1]). Based on exploratory fishing, Fiscus and Mercer (1982) suggested that *O. borealijaponica* could be commercially exploited by a jig fishery from the Gulf of Alaska westward to the Aleutian Islands, and Murata (in Okutani, 1977) indicated that the potential fishery yield of *O. borealijaponica* may be 50,000–200,000 t in an area west of long. 152°E and lat. 40–45°N. If a commercial fishery does develop, accurate life-history information is essential for management purposes.

The general biology and feeding ecology of *Onychoteuthis borealijaponica* have been investigated (Naito et al., 1977b; Okutani and Murata, 1983); however, little information is available on age and growth. Average growth rates have been inferred from length-frequency distributions of sequential jigging samples (Murata and Ishii, 1977). This study suggested that the lifespan for boreal clubhook squid is approximately one year; females grow faster and attain a larger size (370 mm mantle length (ML)) than males (270 mm ML). Growth estimates from driftnet studies (Kubodera et al., 1983; Kubodera, 1986) were inconclusive because length-frequency modes were impossible to detect, possibly because of protracted spawning seasons or variable individual growth rates within a population.

The accuracy and precision of cephalopod growth estimates have been greatly enhanced through the use of daily increments within statoliths (Natsukari et al., 1991). Ageing by counting statolith increments allows the estimation of size at age and may provide information on individual age and growth rates. Hatchdates can be estimated by back calculation of daily increments. Age and growth estimates derived from statolith analysis

[1] DiNardo, G. T., and W. Kwok. In review. Estimates of fish and cephalopod catch in the North Pacific high-seas driftnet fisheries, 1990–91.

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have been obtained from a variety of neritic squid species (see review by Rodhouse and Hatfield, 1990a).

The objectives of this study were to 1) estimate the age and growth of *O. borealijaponica* from statolith microstructural analysis, 2) determine the periodicity of increment formation, 3) statistically compare appropriate growth models fit to the ageing data, 4) determine the distribution of back-calculated hatching dates of *O. borealijaponica* and draw inferences about spawning locations, and 5) determine the relationship between age and maturity stages.

Materials and methods

Taxonomic clarifications

At least five onychoteuthid species are found in the North Pacific: *O. borealijaponica* from subarctic waters; an undescribed species occupying the North Pacific transition zone (~29–40°N, Bigelow, unpubl. data); and three subtropical species of the *O. banksii* complex (Young and Harman, 1987). Juvenile, subadult, and adult *O. borealijaponica* (69–343 mm ML) were separated from other onychoteuthid species based on the number of tentacular hooks (n=25–29) on each club. Identification of *O. borealijaponica* paralarvae (11.5 to 35 mm ML) was based on mantle chromatophore patterns (Bigelow, unpubl. data).

Data collection

Subadults, adults During July–September 1990, *O. borealijaponica* specimens were collected on various research cruises in the North Pacific. Most squid specimens were captured by research drift net (mesh size=48–220 mm stretch mesh) in the western and central North Pacific, but squid jigs were also used to capture specimens from the central and eastern North Pacific (Fig. 1, Table 1). Squid samples were frozen (–20°C) upon capture and returned to the laboratory for analysis.

Paralarvae, juveniles From 5 to 24 August 1991, 39 tows with a modified Cobb trawl were made along meridian 179°30'W between 36°56'N and 46°00'N, and along meridian 174°30'W between 39°00'N and 45°00'N. The trawl was dual warp, with a mouth area of approximately 140 m^2 when fishing and a cod-end liner constructed of 3.2 mm knotless nylon delta mesh (Wyllie Echeverria et al., 1990; Lenarz et al., 1991). Thirty-one oblique night tows (0–150 m) and eight oblique day tows (0–750 m) were conducted. *O. borealijaponica* specimens from eight tows (Fig. 1, Table 1) were sorted on board and immediately frozen (–20°C, juveniles) or fixed in 95% ethyl alcohol (paralarvae).

Laboratory analysis

Dorsal mantle length measurements were made to the nearest millimeter (mm) on thawed specimens. Squids less than 0.5 g were blotted dry and weighed to the nearest 0.001 g, whereas larger specimens were weighed to the nearest 0.1 g. No correction was made for shrinkage of paralarvae from fixation in ethanol, because the species possesses a strong gladius and exhibited minimal shrinkage (<2%). Specimens were sexed and assigned a maturity stage (I: juvenile; II: immature; III: preparatory; IV: maturing; V: mature) based on the appearance and relative size of the gonads and accessory reproductive organs (Lipinski, 1979). Statoliths were dissected from the specimens and stored in 95% ethyl alcohol.

Statolith preparation and microstructural analysis One statolith of the pair was mounted on a microscope slide in Eukitt resin (Calibrated Instruments Inc. 200 Saw Mill Rd., Hawthorne, NY 10532) with the concave side (anterior) facing up. The transparency of paralarval statoliths allowed their examination without further preparation (Fig. 2). The thickening of statoliths from larger squid (>35 mm ML) required that they be ground with fine-grained (1200-grade) carborundum paper and polished with 0.3–µm alumina-silica powder prior to microstructural examination.

Increments were counted beginning at the first visible increment outside the nucleus (Fig. 3A), and continued to the margin of the dorsal dome (Fig. 3B). The diameter of the circular nucleus averaged 28.0 µm (SD=2.4 µm, n=37). The precision of increment counts was assessed by using the coefficient of variation (Chang, 1982). Two nonconsecutive blind increment counts were made on each statolith with transmitted light at a magnification of 1500×. The mean of the two increment counts was accepted if the coefficient of variation was <7.0%, otherwise a third count was conducted. With this criteria, two increment counts were acceptable for 115 statoliths, whereas three increment counts were required for 11 statoliths. Hatching dates were computed by subtracting the mean increment count from the date of capture and were pooled into monthly periods. Increment counts were assumed to represent the individuals' age in days, based on the following results (periodicity of increment deposition) which provided support for the hypothesis that one increment is deposited per day.

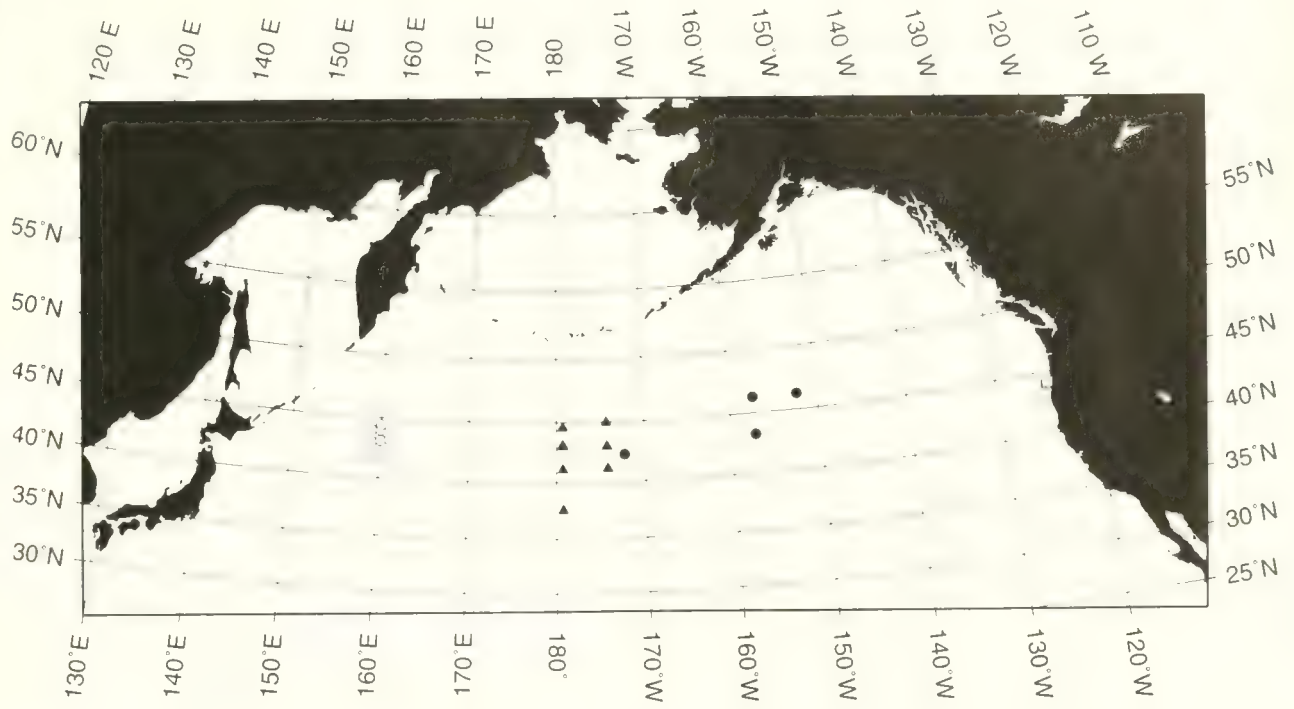

Figure 1

Location of stations in the North Pacific sampled for *Onychoteuthis borealijaponica*: Western North Pacific 1990 (open circles), central North Pacific 1990 (closed circles), central North Pacific 1991 (closed triangles), and eastern North Pacific 1990 (open squares).

Periodicity of increment deposition Three subadult squid caught by jig or trawl in the central North Pacific were placed for two hours in 20 L of seawater containing 250 mg/L oxytetracycline hydrochloride (OTC). After OTC exposure, squid were maintained in a 20–L tank with flowthrough seawater under ambient photoperiod and temperature conditions. Freshly captured live saury (*Cololabis saira*) were introduced as prey, but no feeding was noted or observed. Squids survived up to 61.5 hours in captivity. Statoliths were prepared as above and illuminated with ultraviolet (Fig. 4) and natural light. Under fluorescent light, an ocular marker was aligned with the inner edge of the OTC band. The statolith was then examined under natural light, but increments peripheral to the band were difficult to count. Therefore, to determine the periodicity of increment deposition, statolith growth following OTC exposure was related to the average increment width prior to exposure. The distance from the inner edge of the OTC band to the statolith perimeter was divided by the mean width of increments prior to the OTC band. Three estimates of statolith growth after OTC exposure were made, and the average increment width calculated for 15 increments prior to the OTC band.

Statistical procedures

Mantle length-weight relationships Mantle length-weight regressions were fit to the data by using the model

$$WT(g) = a * ML(mm)^{b} \qquad (1)$$

Separate ML-weight equations were developed for both sexes, and a single equation was used for squid of unknown sex (<60 mm ML).

Fitting of size-at-age data Researchers have used a variety of different models to describe cephalopod growth (e.g., linear, logistic, von Bertalanffy), although the rationale for using a given model is usually not stated. Schnute (1981) proposed a flexible four-parameter model to describe growth which includes most growth models historically used in fisheries research as special cases. The model takes the form

$$Y(t) = \left[y_1^{b} + (y_2^{b} - y_1^{b}) \frac{1 - e^{a(t - t_1)}}{1 - e^{a(t_2 - t_1)}} \right]^{1/b}. \qquad (2)$$

Table 1

Data on samples of *Onychoteuthis borealijaponica* collected for age analysis.

Date	Lat.	Long.	Gear	Depth (m)	Temperature (°C)	*n*	Mantle length (mm)
Western North Pacific							
24 Jul. 1990	42°00'N	158°58'E	Driftnet	0–10	14.9	5	197–316
25 Jul. 1990	43°03'N	158°59'E	Driftnet	0–10	15.5	12	203–311
26 Jul. 1990	44°02'N	158°56'E	Driftnet	0–10	16.1	14	214–343
28 Jul. 1990	44°00'N	160°00'E	Driftnet	0–10	16.5	15	206–339
29 Jul. 1990	43°16'N	159°58'E	Driftnet	0–10	15.7	8	204–233
06 Aug.1990	43°30'N	161°02'E	Driftnet	0–10	16.0	2	275–288
20 Sep.1990	44°45'N	160°03'E	Driftnet	0–10	15.7	1	182
					Total	57	
Central North Pacific							
SAMPLE A							
08 Jul. 1990	42°30'N	172°32'W	Driftnet	0–8.5	14.8	2	165–195
04 Aug.1990	46°30'N	152°30'W	Driftnet	0–8.5	12.1	4	147–180
10 Aug.1990	46°30'N	157°30'W	Driftnet	0–8.5	11.8	7	191–313
12 Aug.1990	43°29'N	157°27'W	Driftnet	0–8.5	14.3	1	343
SAMPLE B							
06 Aug.1991	37°59'N	179°28'W	Cobb	0–154	11.7–24.1	5	11.5–32
06 Aug.1991	37°55'N	179°26'W	Cobb	0–158	11.7–24.1	8	24–35
09 Aug.1991	41°08'N	179°30'W	Cobb	0–130	11.0–20.3	1	42
12 Aug.1991	43°12'N	179°30'W	Cobb	0–775	3.5–16.4	1	58
12 Aug.1991	43°04'N	179°30'W	Cobb	0–156	8.6–15.9	6	69–83
15 Aug.1991	44°59'N	179°27'W	Jig	0–5	12.6	7	119–190
18 Aug.1991	45°00'N	174°31'W	Cobb	0–162	6.8–13.2	4	75–82
20 Aug.1991	43°00'N	174°30'W	Cobb	0–142	8.8–16.5	2	72–78
22 Aug.1991	41 14'N	174°29'W	Cobb	0–730	5.6–21.1	1	66
					Total	49	
Eastern North Pacific							
18 Aug.1990	42°47'N	125°25'W	Jig	0–100	15.1	5	214–251
19 Aug.1990	44°12'N	124°54'W	Jig	0–100	15.9	2	229–236
04 Sep.1990	44°23'N	124°44'W	Jig	0–75	16.4	13	218–312
					Total	20	

where $Y(t)$ is the estimated length or weight at age t, and y_1 and y_2 represent size at two ages t_1 and t_2, which are typically the youngest and oldest individuals in the sample. The estimated parameters a and b describe how the model connects y_1 and y_2. Values of a and b and their 95% confidence intervals lead to the selection of other submodels.

The Schnute model (written in Microsoft Quickbasic) was fit to the size-at-age data (Fig. 5) by nonlinear regression on an IBM-compatable microcomputer. Growth modelling was restricted to individuals from the central North Pacific samples, because of inadequate age representation from the western and eastern North Pacific samples. Paralarval size-at-age estimates were included in the growth models for males and females, because size-at-age results were similar for juvenile (66–83 mm ML) males and females.

Model comparison If we assume that the Schnute model exactly predicts the size of an individual, then the residual sum of squares (RSS) of this full model is an estimate of measurement error. To ascertain if a reduced model with fewer parameters (e.g., 2-parameter exponential) adequately describes the data, the RSS's from the reduced model and full model were compared using an F test statistic:

$$f = \frac{(RSS_R - RSS_F)/(DF_F - DF_F)}{RSS_F/DF_F} \quad (3)$$

with $DF_R - DF_F, DF_F$ degrees of freedom,

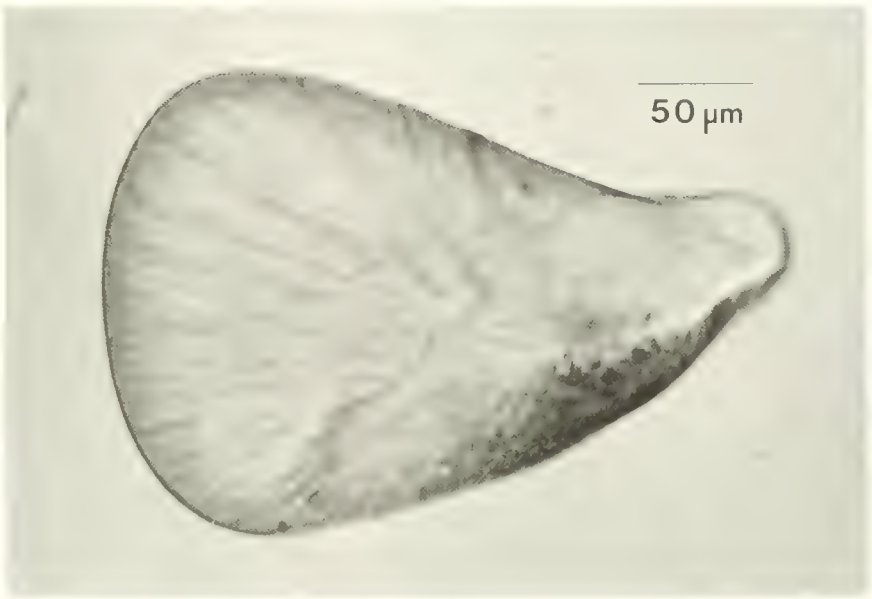

Figure 2

Onychoteuthis borealijaponica. Light micrograph of a transverse section of a statolith from a 11.5-mm mantle length paralarva. Duplicate increment counts were 61 and 63.

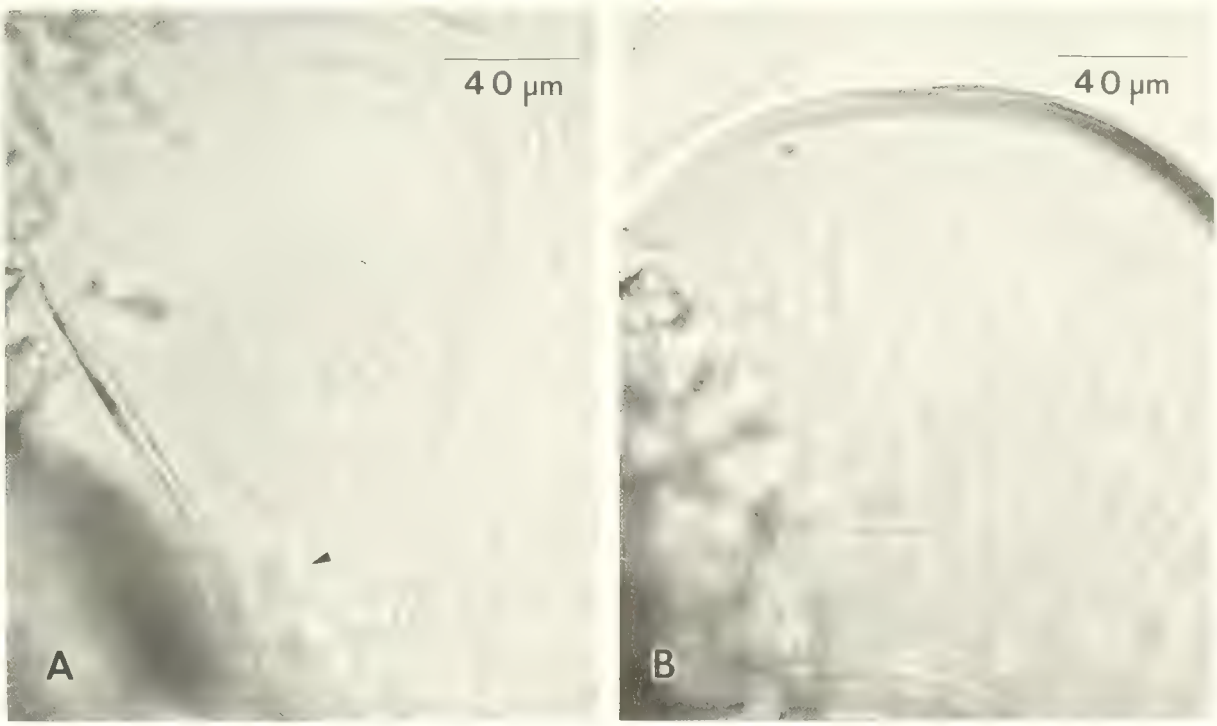

Figure 3

Onychoteuthis borealijaponica. Light micrographs of a ground statolith. (**A**) Increment deposition within early life history. Arrow indicates edge of nucleus. (**B**) Statolith microstructure within dorsal dome region.

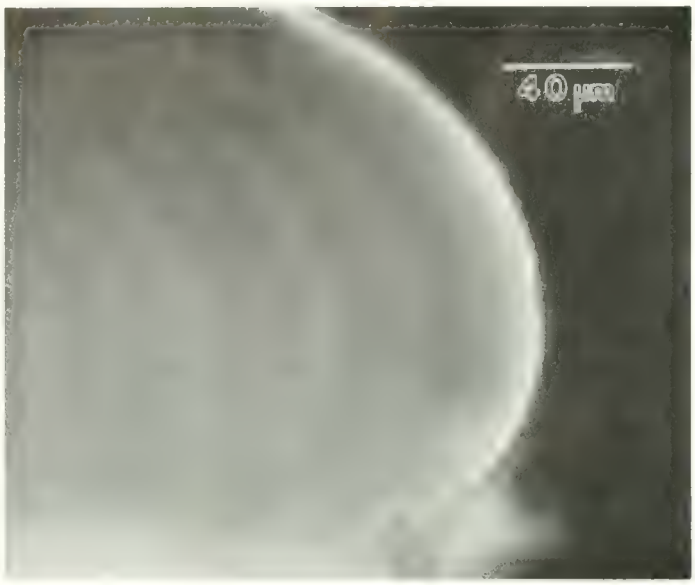

Figure 4

Onychoteuthis borealijaponica. UV micrograph of a ground statolith stained with tetracycline.

where RSS_F is the RSS from the full (Schnute) model, RSS_R is the RSS from the reduced (exponential) model, DF_F is the number of degrees of freedom from the full model, and DF_R is the number of degrees of freedom from the reduced model (Neter et al., 1985).

Differences in the slopes of the ML-weight and size-at-age relationships by sex and geographical location were compared with analysis of covariance (ANCOVA) and F-tests (Sokal and Rolff, 1981). Data were initially ln-transformed, and ANCOVA was used to test for differences in slopes of the linearized equations. Elevations of the linearized equations were compared with F-tests. Analyses were performed on central North Pacific male and female growth data and western North Pacific female data with the assumption that females in the western North Pacific exhibited a similar type of growth as individuals in the central North Pacific. There were too few individuals to test for differences in growth rates

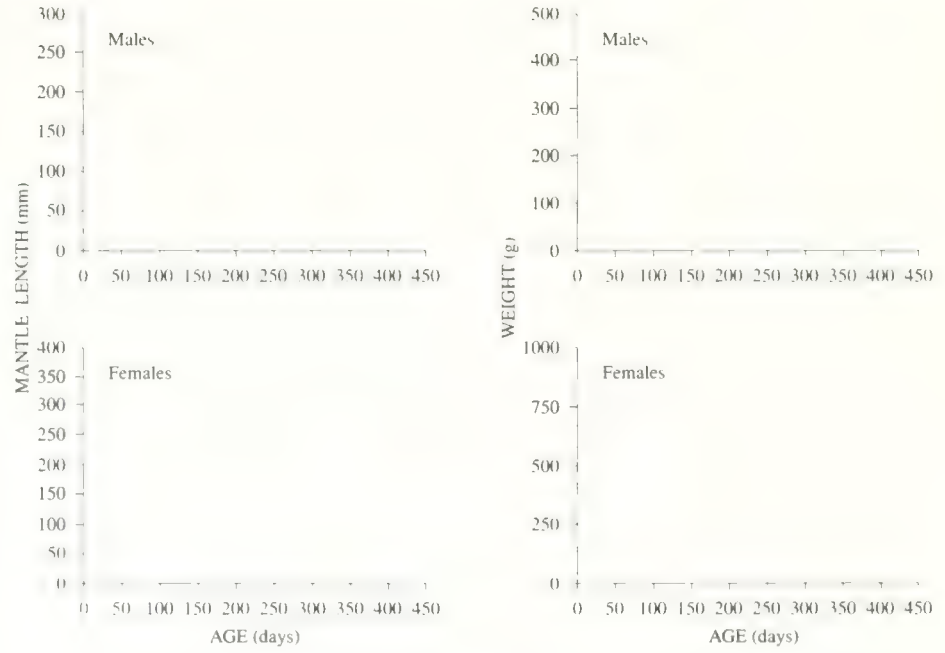

Figure 5

Relation between age (determined by number of increments within statoliths) and mantle length (mm) and weight (g) for male and female *Onychoteuthis borealijaponica*. Western North Pacific 1990 (open circles), central North Pacific 1990 (closed circles), central North Pacific 1991 (closed triangles = juveniles-subadults, open triangles = unknown sex), and eastern North Pacific 1990 (open squares).

of western North Pacific males or eastern North Pacific males and females.

Results

Statolith analysis

Statolith microstructural analysis was applied to 131 squid from the western, central, and eastern North Pacific. Five statoliths (3.8%) were broken or poorly sectioned and excluded from further analysis. The coefficient of variation about the mean for the aged samples (n=126) averaged 3.7% based on 2–3 increment counts for each statolith. No obvious trend existed in the coefficient of variation with the increment count or body size.

Periodicity of increment formation

A fluorescent OTC band was evident in the statoliths of the three squid exposed to oxytetracycline. While increments peripheral to the inner edge of the OTC band could not be reliably counted, the relation between the growth of the statolith, rearing period, and the width of increments prior to the OTC band suggested that increments were deposited daily (Table 2). Statolith growth in the dorsal dome region ranged from 1.4 to 4.3 μm over the rearing period (26–61.5 hr). The average number of increments deposited per day after oxytetracycline exposure was 1.30 (range 1.08–1.52) for the three squid.

Mantle length-weight relationships

The ML-weight relationship for paralarval *O. borealijaponica* from the central North Pacific is represented by the equation

$$WT = 2.484\times10^{-5}\, ML^{3.015}; R^2 = 0.99 (n = 36). \quad (4)$$

The ML-weight relationships for juvenile-adult *O. borealijaponica* from the western, central, and eastern North Pacific are represented by the following equations:

males:

$$WT = 1.873\times10^{-4}\, ML^{2.596}; R^2 = 0.96 (n = 43) \quad (5)$$

females:

$$WT = 3.521\times10^{-5}\, ML^{2.915}; R^2 = 0.99 (n = 68) \quad (6)$$

The slopes of the ML-weight regressions for male and female *O. borealijaponica* were significantly different (P<0.001).

Growth

A good relationship existed between the number of increments within statoliths and squid size for individuals in the central North Pacific (Fig. 5). An exponential model (Table 3, Equation 7) was appropriate to describe the ML-at-age relationship (f=1.82, F=2.49) for females (paralarvae-subadult) in the central North Pacific. A logistic model was appropriate to describe the ML-at-age relationship (f=1.85, F=2.93) for males (paralarvae-adult) in the central North Pacific. However, the oldest individual (394 days, 245 mm ML) was a mature male (stage V) which influenced the type of model selected. Omitting that individual resulted in the selection of an exponential model (f=2.49, F=2.55) over a logistic model (f=4.73, F=2.94) to describe paralarval-subadult growth (Table 3, Equation 8). Exponential models were also fit to weight-at-age data for paralarval-subadult males and females (Table 3, Equations 9 and 10).

Growth in length (% increase in length per day) was similar for males and females (0.80% ML/day) in the central North Pacific, while growth in weight was faster for females (1.90% WT/day) than males (1.40% WT/day). By using the exponential models, mantle length, weight-at-age, and absolute growth

Table 2

Age validation information for *Onychoteuthis borealijaponica* with oxytetracycline (OTC) technique. Width of oxytetracycline band is the distance observed between the fluorescent band and the margin of the statolith. Mean increment width is that of the outer 15 increments formed prior to the OTC band.

No.	ML (mm)	Rearing period (hr)	Width of oxytetracycline band (μm)	Mean increment width (μm)	Estimated increments per day
1	162	26	1.4	1.19	1.08
2	166	61.5	4.3	1.10	1.52
3	175	44	2.8	1.16	1.32

Table 3

Exponential equations for growth of male and female *Onychoteuthis borealijaponica* from the central North Pacific Ocean.

Variable	Age interval (d)	n	Equation	r^2	Equation no.
Length (F)	62–376	36	$mm = 18.41e^{0.00785t}$	0.97	7
Length (M)	62–314	27	$mm = 17.17e^{0.00798t}$	0.89	8
Weight (F)	62–376	36	$g = 0.74e^{0.0188t}$	0.92	9
Weight (M)	62–314	27	$g = 2.19e^{0.0138t}$	0.82	10

rates (*AGR*, mm/day or g/day) were predicted for the initial 365 days (Table 4).

The slopes of the size-at-age regression equations for females from the western North Pacific were significantly different from those for both central North Pacific males and females (Fig. 6, Table 5). Comparisons of regression slopes between central North Pacific males and females revealed no significant differences in length or weight-at-age relationships (P=0.424, P=0.307). Testing of elevations from the central North Pacific male and female data identified a significant difference (P<0.001, Table 5); therefore, males and females in the central North Pacific grow in length and weight at a similar rate, but females display a significantly greater size at age than males (Table 4).

Back-calculated hatching dates

Backcalculation of hatching dates demonstrated that *O. borealijaponica* hatched in all months except March (Fig. 7). The distribution of hatching dates was not necessarily related to spawning intensity, as more subadult squid were available for age analysis than paralarvae and juveniles. Subadult and adult squid captured from July to September in the North Pacific had similar hatch dates as samples collected from the western (August–February), central (July–February), and eastern North Pacific (August–November). Paralarval and early juvenile squid captured in the central North Pacific during August 1991 were estimated to have hatched between February and June, 1991.

Maturity stage-age relationships

Maturity stages were closely related to squid size for all three sampling areas; males, however, matured at a smaller size than females (Fig. 8). Females and males recruit to the driftnet fishery after attaining maturity stages III and IV, respectively. No mature females (stage V) were captured by any sampling

Table 4

Growth of central North Pacific *Onychoteuthis borealijaponica* predicted by the exponential equations based on statolith analysis. Absolute growth rates (*AGR*) are given in mm or g per day.

	Males				Females			
Estimated age (days)	Mantle length (mm)	AGR_L	Weight (g)	AGR_W	Mantle length (mm)	AGR_L	Weight (g)	AGR_W
50	25.6	0.20	4.4	0.06	27.3	0.21	1.9	0.04
75	31.2	0.25	6.1	0.09	33.2	0.26	3.0	0.06
100	38.1	0.31	8.7	0.12	40.3	0.32	4.8	0.09
125	46.5	0.37	12.2	0.17	49.1	0.39	7.7	0.15
150	56.8	0.46	17.3	0.24	59.7	0.47	12.4	0.24
175	69.4	0.56	24.3	0.34	72.7	0.57	19.8	0.38
200	84.7	0.68	34.3	0.48	88.4	0.70	31.7	0.60
225	103.4	0.83	48.5	0.67	107.5	0.85	50.8	0.96
250	126.2	1.01	68.4	0.95	130.8	1.03	81.3	1.54
275	154.1	1.23	96.5	1.34	159.2	1.25	130.0	2.47
300	188.1	1.51	136.1	1.89	193.7	1.53	208.0	3.95
325	229.6	1.84	192.1	2.66	235.7	1.86	332.8	6.31
350	280.3	2.24	271.0	3.75	286.7	2.26	532.5	10.10
365	316.0	2.57	337.3	4.66	323.2	2.51	706.9	13.42

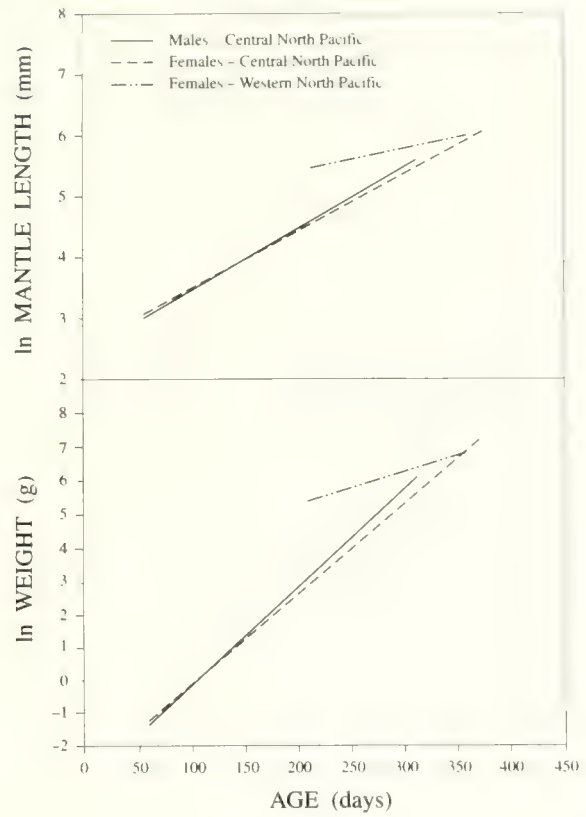

Figure 6

Log-linear growth models for male and female *Onychoteuthis borealijaponica*.

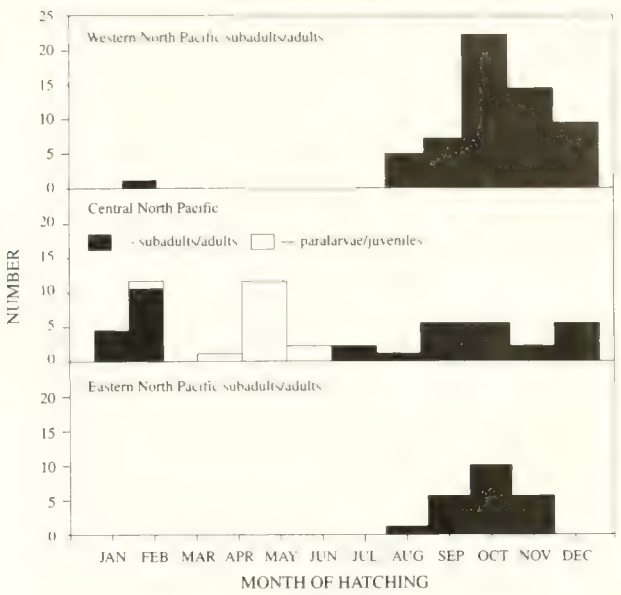

Figure 7

Estimated hatch-date distributions by month for *Onychoteuthis borealijaponica*.

method. There was some evidence that males (stage IV–V) and females (stage III–IV) in the western North Pacific were younger than similar stage individuals from the central and eastern North Pacific.

Discussion

The data presented provide support for the one-increment-deposited-per-day hypothesis within the statoliths of *Onychoteuthis borealijaponica* although further work is required to rigorously test the hypothesis. Tetracycline was incorporated into the statolith, but the animals did not feed and survival was not sufficiently long enough (2–3 days) to provide a rigorous test on the rate of increment deposition. Validation of the daily increment hypothesis has come from tetracycline labeled statolith experiments with several neritic squid species (*Illex illecebrosus*, Dawe et al., 1985, *Alloteuthis subulata*, Lipinski, 1986, *Todarodes pacificus*, Nakamura and Sakurai, 1991). Future statolith validation experiments with

Table 5

Comparisons of *Onychoteuthis borealijaponica* growth equations based on analysis of covariance.

	Slope (F)	Elevation (F)	P
Length-at-age comparisons			
Central North Pacific, male vs. female	0.647		0.424
		1002.4	<0.001
Western North Pacific female vs. central Pacific female	62.9		<0.001
Western North Pacific female vs. central Pacific male	62.2		<0.001
Weight-at-age comparisons			
Central North Pacific, male vs. female	1.063		0.307
		1121.1	<0.001
Western North Pacific female vs. central Pacific female	65.9		<0.001
Western North Pacific female vs. central Pacific male	66.6		<0.001

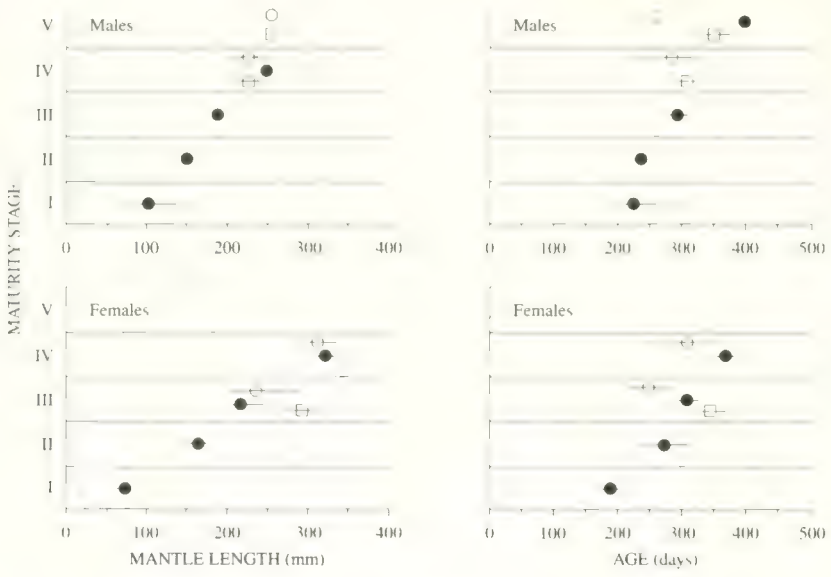

Figure 8

Relationship between mantle length and number of increments in statoliths and male and female maturity stage: western North Pacific (open circles), central North Pacific (closed circles), and eastern North Pacific (open squares). Ranges are represented by horizontal bars.

active oceanic squids (e.g., Onychoteuthidae, Ommastrephidae) may require substantial maintenance facilities to support long-term survival.

Although the rate of increment deposition derived by the statolith marking experiment should be considered preliminary, indirect evidence was obtained to suggest that increments were formed daily. The hypothesis that the lifespan is 1 year (Murata and Ishii, 1977; Naito et al., 1977b) was supported by the present data where only 4 of the 126 individuals aged had more than 365 increments within the statolith. In addition, back-calculated hatch dates (July–February) of post-recruit individuals exploited in the *O. borealijaponica* jig and *Ommastrephes bartramii* squid driftnet fishery were consistent with information on spawning (fall-winter) reported in the literature (Murata et al., 1976; Murata and Ishii, 1977; Naito et al., 1977b). This study suggests that spawning for *O. borealijaponica* occurs year round. While subadult *O. borealijaponica* are distributed in subarctic waters, evidence from the distribution of paralarvae, juveniles, and sexually mature females suggests that spawning may occur to the south of the subarctic boundary in the North Pacific transition zone (30–42°N, terminology after Roden, 1991). In the central and eastern North Pacific, *O. borealijaponica* paralarvae and juveniles have been recorded from this study (38°N, 179°30'W°) and the coast of California (~33°N, Young, 1972), respectively. In the western North Pacific, spawning may occur in waters of the Kuroshio Current and Kuroshio Countercurrent (Murata and Ishii, 1977; Naito et al., 1977a) or between the Kuroshio and Oyashio fronts. Onychoteuthid paralarvae have been captured from both the Kuroshio Current and Kuroshio Countercurrent (Okutani, 1968, 1969, 1975); however, distributional evidence is inconclusive because of the taxonomic uncertainties of the specimens captured. Spawning may occur in the transitional area between the Kuroshio and Oyashio fronts, as sexually mature and copulated females have been captured off Hokkaido, Japan (42°30'N, 150°40'E and 42°15'N, 144°25'E, Murata et al., 1981).

The ML-weight relationships obtained in this study for the western, central, and eastern North Pacific were similar to the values previously given for *O. borealijaponica* captured off Japan (Murata and Ishii, 1977). Slope values obtained for the ML-weight relationships (males=2.596, females=2.915) were similar to other active oceanic squids having thick muscular mantle walls. Paralarval *O. borealijaponica* had a higher slope value (3.015) than older males and females, consistent with previous results for loliginid squids and benthic octopods (Forsythe and Van Heukelem, 1987).

There is no clear consensus on the type of model which best describes cephalopod growth, although several studies argue against the use of asymptotic models, such as Gompertz or von Bertalanffy (Forsythe and Van Heukelem, 1987; Saville, 1987). Exponential models have been typically used to describe the growth of field caught and laboratory reared paralarval squid (Yang et al., 1986; Balch et al., 1988; Forsythe and Hanlon, 1989; Bigelow, 1992, 1993). For growth estimates derived from statolith analysis, a linear model is frequently used because growth is analyzed over a short segment of the cephalopod's life history, such as post recruitment to a fishery (Rosenberg et al., 1980; Radtke, 1983; Rodhouse and Hatfield, 1990b) or habitat (Jackson and Choat, 1992).

Since the Schnute model encompasses a wide range of growth models, it can be used to system-

atically assess the type of growth model which best describes the data. A statistical comparison of several growth models found that growth in *O. borealijaponica* from the paralarval to subadult size range could be sufficiently described with an exponential model, though there was weak evidence that a logistic model may be sufficient to describe growth in males from the paralarval to adult size range. The most appropriate growth model (exponential or logistic) for the entire life cycle of *O. borealijaponica* will emerge when sexually mature males and females are aged.

Estimated growth rates from this study were higher than estimates derived from length-frequency analysis of fisheries data (Murata and Ishii, 1977). Growth estimates based on length-frequency analysis with time often provide evidence of decreased growth rate, which is usually described by an asymptotic model (Patterson, 1988). Length-frequency analysis may be inappropriate for estimating growth in cephalopods (Jackson and Choat, 1992), either because 1) cohorts are difficult to detect because spawning occurs throughout the year, 2) variable individual growth rates produce Lee's phenomenon (Ricker, 1975), or 3) samples of a migrating population are taken at a point along the migration route, which results in overestimating growth in young squid and underestimating growth in older squid.

Growth data presented for *O. borealijaponica* from the central North Pacific provide a useful comparison of growth between males and females. The exponential models predict that males and females grow in length at similar rates (0.80% ML/day), but females grow faster in weight (1.90% WT/day) than do males (1.40% WT/day). These rates correspond closely with the average growth rates of similar sized squids from temperate waters (e.g., *Illex illecebrosus*, O'Dor, 1983; *I. argentinus*, Rodhouse and Hatfield, 1990b).

The most significant advantage of using statolith ageing techniques is the ability to produce individual rather than population statistics. Using statolith analysis, spatial variations in size at age, growth parameters, and maturity stage at age were observed between *O. borealijaponica* individuals from the western and central North Pacific. Little is known concerning genetic variation and stock structure of *O. borealijaponica* in the North Pacific; however, female squid in the western North Pacific were found to grow faster than both male and female squid in the central North Pacific and were younger at maturity stages III and IV than central North Pacific females. Apparent growth rate and maturity stage differences may be related to water temperatures or food availability during the paralarval stage. Forsythe and Hanlon (1989) showed that temperature had a pronounced effect on the increase in length and weight of the squid *Loligo forbesi*. In their laboratory study, a temperature increase of 1°C increased the growth in length and weight of paralarval squid 0.5% and 2.0% per day, respectively. Subadults in the western Pacific may have hatched in the warm Kuroshio Current or in productive transition waters between the Kuroshio and Oyashio fronts. Paralarvae hatched in the western North Pacific may therefore experience higher temperatures or a greater abundance of prey species, or both, than paralarvae hatched in the central North Pacific, which could explain the observed spatial differences in growth.

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Literature cited

Balch, N., A. Sirois, and G. V. Hurley.
1988. Growth increments in statoliths from paralarvae of the ommastrephid squid *Illex* (Cephalopoda: Teuthoidea). Malacologia 29:103–112.

Bigelow, K. A.
1992. Age and growth in paralarvae of the mesopelagic squid *Abralia trigonura* based on daily growth increments in statoliths. Mar. Ecol. Prog. Ser. 82:31–40.
1933. Hatch dates and growth of *Ommastrephes bartramii* paralarvae from Hawaiian waters as determined from statolith analysis. *In* T. Okutani (ed.), Proceedings of the international symposium on the recent advances in cephalopod fisheries biology, p. 15–24 University Press, Tokai, Japan.

Chang, W. Y. B.
1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39:1208–1210.

Dawe, E. G., R. K. O'Dor, P. H. Odense, and G. V. Hurley.
1985. Validation and application of an ageing tech-

nique for short-finned squid (*Illex illecebrosus*) J. Northwest Atl. Fish. Sci. 6:107–116.

Fiscus, C. H., and R. W. Mercer.
1982. Squids taken in surface gillnets in the North Pacific Ocean by the Pacific salmon investigations program 1955–72. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-FNWC-28, 31 p.

Forsythe, J. W., and W. F. Van Heukelem.
1987. Growth. *In* P. R. Boyle (ed.), Cephalopod life cycles, vol. II, p. 135–156. Academic Press, London.

Forsythe, J. W., and R. T. Hanlon.
1989. Growth of the eastern Atlantic squid, *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda). Aquat. Fish. Manage. 20:1–14.

Jackson, G. D., and J. H. Choat.
1992. Growth in tropical cephalopods: an analysis based on statolith microstructure. Can. J. Fish. Aquat. Sci. 49:218–228.

Kubodera, T.
1986. Relationships between abundance of epipelagic squids and oceanographical-biological environments in the surface waters of the subarctic Pacific in summer. Int. North Pac. Fish. Comm. Bull. 47:215–228.

Kubodera, T., W. G. Pearcy, K. Murakami, T. Kobayashi, J. Nakata, and S. Mishima.
1983. Distribution and abundance of squids caught in surface gillnets in the subarctic Pacific., 1977–1981. Mem. Fac. Fish. Hokkaido Univ. 30(1/2): 1–49.

Lenarz, W. H., R. J. Larson, and S. Ralston.
1991. Depth distributions of late larvae and pelagic juveniles of some fishes of the california current. CalCOFI Rep. 32:41–46.

Lipinski, M.
1979. Universal maturity scale for the commercially important squids. The results of maturity classification of the *Illex illecebrosus* population for the years 1973–77. ICNAF Res. Doc. 79/2/38, Serial 5364, 40 p.
1986. Methods for the validation of squid age from statoliths. J. Mar. Biol. Assoc. U.K. 66:505–525.

Murata, M., and M. Ishii.
1977. Some information on the ecology of the oceanic squid, *Ommastrephes bartrami* (Lesueur), and *Onychoteuthis borealijaponicus* Okada, in the Pacific Ocean off Northeastern Japan. Bull. Hokkaido Reg. Fish. Res. Lab 42:1–23. (In Japanese; English abstract.)

Murata, M., T. Ishii, and H. Araya.
1976. The distribution of the oceanic squids, *Ommastrephes bartramii* (Lesueur), *Onychoteuthis borealijaponicus* Okada, *Gonatopsis borealis* Sasaki and *Todarodes pacificus* Steenstrup in the Pacific Ocean off north-eastern Japan. Bull. Hokkaido Reg. Fish. Res. Lab 41:1–29. (In Japanese; English abstract.)

Murata, M., M. Ishii, and M. Osako.
1981. Some information on copulation of the oceanic squid *Onychoteuthis borealijaponica* Okada. Bull. Jap. Soc. Sci. Fish. 48:351–354. (In Japanese; English abstract.)

Naito, M., K. Murakami, T. Kobayashi, N. Nakayama, and J. Ogasawara.
1977a. Distribution and migration of oceanic squids (*Ommastrephes bartramii*, *Onychoteuthis borealijaponicus*, *Berryteuthis magister*, and *Gonatopsis borealis*) in the western subarctic Pacific region. Spec. Vol., Res. Inst. N. Pac. Fish., p. 321–337. (In Japanese; English abstract.) (Engl. transl. by W. G. Van Campen, 1991, 23 p., Translation No. 144; available Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar Fish. Serv., NOAA, 2570 Dole St., Honolulu, HI 96822–2396.)

Naito, M., K. Murakami, and T. Kobayashi.
1977b. Growth and food habit of oceanic squids (*Ommastrephes bartramii*, *Onychoteuthis borealijaponicus*, *Berryteuthis magister* and *Gonatopsis borealis*) in the western subarctic Pacific region. Spec. Vol., Res. Inst. N. Pac. Fish., p. 339–351. (In Japanese; English abstract.) (Engl. transl. by W. G. Van Campen, 1991, 19 p., Translation No. 147; available Honolulu Lab., Southwest Fish. Sci. Cent., Natl. Mar Fish. Serv., NOAA, 2570 Dole St., Honolulu, HI 96822–2396.)

Nakamura, Y., and Y. Sakurai.
1991. Validation of daily growth increments in statoliths of Japanese common squid *Todarodes pacificus*. Nippon suisan Gakkaishi 57(11):2007–2011.

Natsukari, Y., E. Dawe, and M. Lipinski.
1991. Interpretation of data. Practical procedures of squid ageing using statoliths. A laboratory manual. Section 2. *In* P. Jereb, S. Ragonese, S. von Boletzky (eds.), Squid age determination using statoliths. Proc. Internat. Workshop, Instituto di Tecnologia della Pesca e del Pescato (ITPP-CNR), Mazara del Vallo, Italy, 9–14 Oct. 1989. N.T.R.-I.T.P.P. Spec. Publ. 1

Neter, J., W. Wasserman, and M. H. Kutner.
1985. Applied linear statistics, 2nd ed. Richard D. Irwin, Inc., IL, 1127 p.

O'Dor, R. K.
1983. *Illex illecebrosus*. In P. R. Boyle, (ed.), Cephalopod life cycles, vol. I, p. 175–199. Academic Press, London.

Okutani, T.
1968. Studies on early life history of decapodan Mollusca-III. Systematics and distribution of larvae of decapod cephalopods collected from the sea surface on the Pacific coast of Japan 1960–1965. Bull. Tokai Reg. Fish. Res. Lab. 55:9–57.
1969. Studies on early life history of decapodan Mollusca- IV. Squid larvae collected by oblique hauls of a larva net from the Pacific coast of eastern Honshu, during the winter seasons. Bull. Tokai Reg. Fish. Res. Lab. 58:83–96.
1975. Studies on early life history of decapodan Mollusca-V. Systematics and distribution of epipe-

lagic larvae of decapod cephalopods in the southwestern waters of Japan during the summer in 1970. Bull. Tokai Reg. Fish. Res. Lab. 83:45–96.

1977. Stock assessment of cephalopod resources fished by Japan. FAO Fish. Tech. Paper 173:1–62.

Okutani, T., and M. Murata.

1983. A review of the biology of the oceanic squid *Onychoteuthis borealijaponica*. Memoirs of the Natl. Mus. of Victoria 44:189–195.

Patterson, K. R.

1988. Life history of Patagonian squid *Loligo gahi* and growth parameter estimates using least-squares fits to linear and von Bertalanffy models. Mar. Ecol. Prog. Ser. 47:65–74.

Radtke, R. L.

1983. Chemical and structural characteristics of statoliths from the short-finned squid *Illex illecebrosus*. Mar. Biol. 76:47–54.

Ricker, W. E.

1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 91:1–382.

Roden, G. I.

1991. Subarctic-subtropical transition zone of the North Pacific: large-scale aspects and mesoscale structure. *In* J. A. Wetherall (ed.), Biology, oceanography, and fisheries of the North Pacific transition zone and subarctic frontal zone, p. 1–38. NOAA Tech. Rep. NMFS 105, 111 p.

Rodhouse, P. G., and E. M. C. Hatfield.

1990a. Age determinations in squid using statolith growth increments. Fish. Res. (Amst.) 8:323–334.

1990b. Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea: Ommastrephidae). Philos. Trans. R. Soc. Lond. B. Biol. Sci. 329:229–241.

Rosenberg, A. A., K. F. Wiborg, and I. M. Bech.

1980. Growth of *Todarodes sagittatus* (Lamarck) (Cephalopoda, Ommastrephidae) from the northeast Atlantic, based on counts of statolith growth rings. Sarsia 66:53–57.

Saville, A.

1987. Comparisons between cephalopods and fish of those aspects of the biology related to stock management. *In* P. R. Boyle (ed.), Cephalopod life cycles, vol. II, p. 277–290. Academic Press, London.

Schnute, J.

1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38:1128–1140.

Sokal, R. R., and F. J. Rohlf.

1981. Biometry. W.H. Freeman, San Francisco.

Wyllie Echeverria, T., W. H. Lenarz, and C. A. Reilly.

1990. Survey of the abundance and distribution of pelagic young-of-the-year rockfishes, *Sebastes*, off central California. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-147, 125 p.

Yang, W. T., R. F. Hixon, P. E. Turk, P. E. Krejci, W. H. Hulet, and R. T. Hanlon.

1986. Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle. Fish. Bull. 84:771–797.

Young, R. E.

1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. Smithsonian Contr. Zool. 97:1–159.

Young, R. E., and R. F. Harman.

1987. Descriptions of the larvae of three species of the *Onychoteuthis banksii* complex from Hawaiian waters. Veliger 29(3):313–321.

Diet of the Kemp's ridley sea turtle, *Lepidochelys kempii*, in New York waters

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Abstract.— A review of previous studies on Kemp's ridley sea turtle (*Lepidochelys kempii*) diet was combined with information on the diet of the species in the coastal waters of New York State. Juvenile Kemp's ridleys occupy coastal Long Island, New York waters during the summer and early autumn months. Both fecal and intestinal samples collected between 1985 and 1989 were analyzed to obtain information on the diet of this endangered species. Fecal and intestinal sample analysis, as well as information from previous studies, indicated that juvenile Kemp's ridleys primarily consume crabs. Walking crabs of the genera *Libinia* and *Cancer* appear to be the primary food sources for the species in New York waters.

The Kemp's ridley sea turtle, *Lepidochelys kempii*, was placed on the United States endangered species list in December 1970 and was listed as one of the twelve most endangered species in the world by the International Union for the Conservation of Nature and Natural Resources in 1986 (Federal Register, 1989; Marine Turtle Newsletter, 1989). Despite a recent increase in research on the Kemp's ridley, little attention has been focused on its feeding habits. An understanding of the dietary requirements and available food resources for the Kemp's ridley is a critical component in the future management and protection of this species' habitats.

While occasional glimpses into the composition of Kemp's ridley diets have been obtained, detailed quantified examinations of the species' diet have only rarely been undertaken (Table 1). In one of the earliest accounts of the diet of Kemp's ridleys, De Sola and Abrams (1933) dissected "two foot specimens" from the Georgia coast and described the main dietary component as *Platyonichus ocellatus*, later renamed the spotted lady crab, *Ovalipes stephensonii* (Williams, 1984).

Two decades later, the first published record describing the diet of the Kemp's ridley in the Gulf of Mexico was produced (Liner, 1954). In that study, gastrointestinal contents of eight *L. kempii* ranging in size from 3.2 kg to 26.6 kg were examined. All the turtles had consumed portunid crabs (*Callinectes* sp.) and occasional barnacles. Dobie et al. (1961), elaborating on the findings of Liner (1954), reported that small molluscs, plant parts, and mud were also contained in the gastrointestinal tracts of two of Liner's turtles. The molluscs included gastropods (*Nassarius* sp.) and bivalves of the genera *Nuculana*, *Corbula*, and probably *Mulinia*.

In Virginia, Hardy (1962) dissected a single specimen and found that the digestive tract contained 95% *Callinectes* sp. and one swimmerette was identified as that of the blue crab, *C. sapidus*. Research conducted in the waters of Chesapeake Bay, Virginia, by Lutcavage (1981) indicated that three Kemp's ridley carcasses had both blue crabs and Atlantic rock

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Table 1

Compilation of available diet studies of Kemp's ridley sea turtles (*Lepidochelys kempii*) published from 1933 to 1991. The studies are ordered from north to south and east to west. Marquez (1973) is cited from Pritchard and Marquez (1973).

Author(s)	Location	Diet components	Life stage
Hardy (1962)	Chesapeake Bay	Blue crabs	Juvenile
Lutcavage (1981)	Chesapeake Bay	Blue crabs	Juvenile
Belmund et al. (1987)	Chesapeake Bay	Rock and blue crabs	Juvenile
DeSola and Abrams (1933)	Coastal Georgia	Crabs (*Ovalipes* spp.)	Not given
Carr (1942)	Florida	Calico crabs	Juvenile
Liner (1954)	Louisiana	Blue crabs	Juvenile
Dobie et al. (1961)	Louisiana	Crabs, whelks, clams	Juvenile
Shaver (1991)	Texas	Various crab species	Juvenile
Marquez (1973)	Tampico, Mexico	Crustaceans, fish, molluscs	Adult

crabs (*Cancer irroratus*) in their digestive tracts.

Recently, Shaver (1991) found that Kemp's ridleys in coastal Texas waters preyed mainly on crabs. The most commonly ingested species was the speckled crab (*Arenaeus cribrarius*). Many other crab species were recorded by Shaver, including purse crabs (*Persephonia* sp.), spider crabs (*Libinia* sp.), and blue crabs (*Callinectes* sp.).

During the past decade, the role of the northeastern coast of the United States in the life cycle of Kemp's ridleys has received considerable attention (Carr, 1980; Morreale and Standora, 1990[1]; Burke et al., 1991). The northeastern coast includes the New York area which contains over 300 km of shoreline, mainly the coastline of Long Island. Long Island has a variety of marine habitats, including the shallow, enclosed waters of the Peconic and southern bays, the deeper waters of Long Island Sound, and the Atlantic Ocean (Fig. 1). Each year Kemp's ridleys begin inhabiting the Long Island area during July (Morreale and Standora, 1989[2]; Morreale and Standora, 1990[1]). To date, all Kemp's ridleys encountered in Long Island have been juveniles (straight-line carapace length from 22 cm to 42 cm x=29.8 cm, SD=3.7 cm [Morreale and Standora, 1989[2], 1990[1]]). This size class of turtles represents a range of ages from 3 to 7 years (Zug and Kalb, 1989).

Between July and early October these young Kemp's ridleys are active within the estuarine waters (Long Island Sound and the Peconic Bays) and the southern bays. Kemp's ridley growth rates as high as 25% body weight per month indicate that waters around Long Island, New York, provide abundant food resources for the maintenance and growth of the juvenile turtles (Standora et al., 1989; Burke, 1990). During October the turtles begin moving out of the estuaries and into the ocean. Long distance recaptures of Kemp's ridley, green (*Chelonia mydas*), and loggerhead (*Caretta caretta*) sea turtles tagged near Long Island indicate that some turtles emigrate to the southeastern United States (Morreale and Standora, 1989[2]; Burke, 1990; Morreale and Standora, 1990[1]). Kemp's ridleys that do not emigrate by late November are likely to become cold-stunned (Burke et al., 1991). Cold-stunning, or severe hypothermia, occurs when ambient water temperatures fall below 10°C (Schwartz, 1978). Cold-stunning causes turtles to become torpid and buoyant, and eventually results in death. In Long Island, declining water temperatures usually reach 10°C during early December.

The cold-stunning phenomenon, other types of strandings, and live captures of sea turtles during commercial fishing operations can be utilized as sources of turtles for dietary studies. The goal of the current study is to provide a quantitative description of the diet of Kemp's ridleys in the northeastern United States based on gut contents from carcasses, previously preserved dietary samples, and feces from live turtles.

Materials and methods

The dietary components of the Kemp's ridley were assessed by using two separate approaches. First, fecal samples were collected from live turtles and examined for their constituents. Second, complete gastrointestinal contents were removed from dead turtles and identified. Samples were obtained from

[1] Morreale, S. J., and E. A. Standora. 1990. Occurrence, movement and behavior of Kemp's ridley and other sea turtles in New York waters. Annual report to the New York State, Dep. Environmental Conservation, April 1989–April 1990.

[2] Morreale, S. J., and E. A. Standora. 1989. Occurrence movement and behavior of the Kemp's ridley and other sea turtles in New York waters. Annual report to the New York State, Dep. Environmental Conservation, April 1988–April 1989.

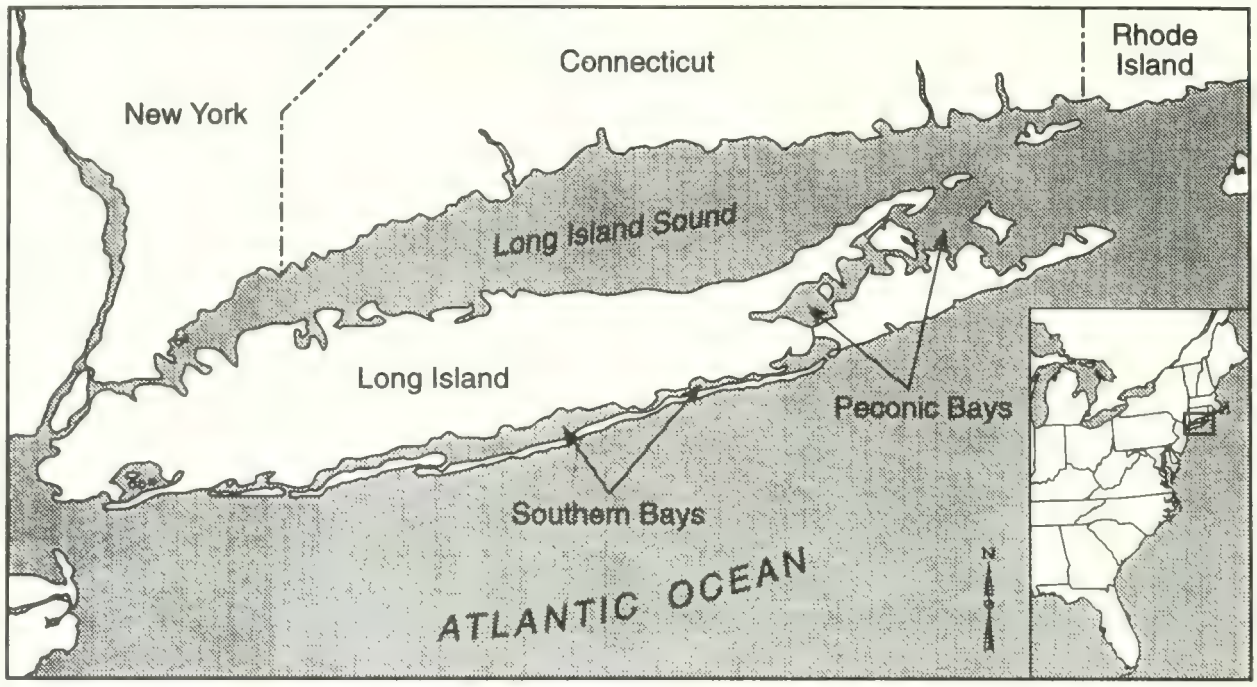

Figure 1

The waters from which Kemp's ridley sea turtles, *Lepidochelys kempii*, were obtained for this study can be divided into four habitats: Long Island Sound, where most of the stranded turtles were recovered; the Atlantic Ocean, which was the habitat of two turtles in the study; the southern bays, where one live capture and one boat-hit turtle were recovered; and the Peconic Bay system, where most of the turtles for the fecal analysis and several turtles for the digestive tract analysis wree recovered.

turtles encountered in New York waters from 1985 through 1989.

Nineteen fecal samples were obtained. Fourteen were collected during 1989, three during 1988, and two during 1987. Of these fecal samples, 17 were obtained from live turtles captured during warmer months (June to October) and two samples were retrieved from revived, cold-stunned turtles in late November. Captured turtles were obtained from local commercial fishermen who were asked to retain turtles caught incidentally in fishing gear (predominantly pound nets). After the fishermen docked, they called a 24-hour number to reach a biologist, who generally picked up the turtle while the fishermen were still unloading their catch. All noncold-stunned Kemp's ridleys received from commercial fisheries in Long Island were alive and apparently healthy.

All turtles were weighed and measured upon return to the laboratory. Each turtle was then allowed to swim freely in an individual 2100–liter tank and was offered either squid or clam meat. Most Kemp's ridleys accepted the food offerings, but many fed only after the food was dangled in front of them for as long as 2–3 hours. Feeding often induced defecation within a relatively short time.

Tanks were checked at least three times a day for the appearance of feces. Filter intakes in the tanks were elevated and covered, except for small holes, to insure against sample loss. When feces were observed, they were immediately removed and placed in individual sample jars. If a turtle did not defecate within 24 hours of being placed in captivity, it was given an enema of dioctyl sodium sulfosuccinate (Disposaject brand, Pitman-Moore Inc.). If a fecal sample was still not obtained after another 24 hours, the turtle was released.

The rate of food passage was examined during this study to insure that samples were not polluted with prey items eaten while the turtles were in the fishermen's nets. Gut passage rates were determined for two Kemp's ridleys by feeding them declawed lobsters (*Homarus americanus*). Lobster was used as a tracer because it has never been reported as a prey item and is consumed relatively readily by the turtles. By monitoring fecal output, the amount of time between ingestion of the lobster

and its first appearance in the feces was determined.

All fecal samples collected for dietary analysis were immediately placed in preservative. For fecal samples obtained during 1989, animal components were preserved as described by Zinn (1984) and algae were preserved in Transeau's solution (10 parts formalin/30 parts ethanol/60 parts distilled H_2O/25 mg $CuSO_4$/L). Feces obtained prior to 1989 were preserved in 10% formalin.

Analysis of the fecal samples was conducted in January 1990, after all the samples were collected. The samples were removed from the preservative and air dried for 24 hours on wire mesh in an enclosed hood. The samples were then placed in a U.S. standard number-5 mesh (4 mm) sieve and pieces smaller than 4 mm were separated out by shaking the sample in a Tyler RO-TAP testing sieve shaker for three minutes. Pieces smaller than 4 mm were not identified because of the difficulty of assigning them to a meaningful category. The amount of sample lost because of this constraint was never greater than 5% for any given sample.

Each fecal sample was examined under a dissecting microscope and each fragment of the sample was identified to the lowest taxon possible. Fragments belonging to the same taxonomic level were grouped. A list of components (e.g., one species of crab is one component) was compiled for each sample and the data were analyzed to determine the percentage of turtles in which each component occurred. Less than 1% of the fragments could not be assigned to a taxonomic category.

For the 1989 samples only, the relative amount of each dietary component was determined by oven drying each component from each sample for 48 hours at 60°C and weighing it. The dry weights were then used to determine the relative importance of the different dietary components in each turtle's fecal sample. Dry weight analysis was conducted by finding the percentage of each sample weight represented by each component and then determining the mean for that component. This technique of analyzing dry weights as a percentage eliminated over- or under-representation of large or small fecal samples.

A second method of determining dietary components was analysis of gastrointestinal contents from stranded, dead turtles. Stranded Kemp's ridleys died from a number of causes: cold-stunning, boat collisions, entanglement in a gill net, and natural and unknown causes. Whenever possible, each stranded turtle was weighed, measured (straight-line carapace length) and dissected. Following removal, intestinal contents were placed in 95% ethanol (1985), 10% formalin (1986–1988), or treated in the same manner as the fecal samples (1989). Identification of intestinal tract contents was performed during 1990. All components of each sample were identified to the lowest taxon possible, generally to species. These data were used to determine the percentage of turtles in which the components occurred.

Results

The food passage rate analysis indicated that lobster was retained within the digestive tracts of the two Kemp's ridleys for seven and eight days. Because fecal samples were obtained within 48 hours of receiving a turtle from a fisherman, we believe the possibility of samples having been "contaminated" by items eaten while the turtles were in the fishermen's nets is minimal.

Mean straight-line carapace length for the 19 turtles in the fecal analysis study was 32.3 cm (range=24.7 to 42.7 cm, SD=4.87). Eighteen of the 19 turtles consumed crabs (Fig. 2). Mollusc species were found in 26% of the fecal samples and algae were found in 11% of the Kemp's ridley feces. Natural and synthetic debris were present in 21% and 11% of the feces respectively.

Crab species that were identified included nine-spined spider crabs, Atlantic rock crabs, and lady crabs (*Ovalipes ocellatus*). Further examination of only the crab portion of the feces revealed that 58% of the turtles had consumed spider crabs, 36% had eaten rock crabs, and 16% had consumed lady crabs.

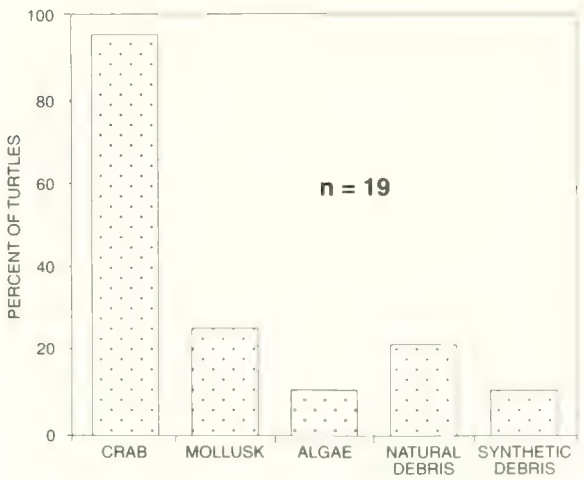

Figure 2

Percent occurrence of various prey items identified in the feces of 19 Kemp's ridley sea turtles (*Lepidochelys kempii*) that were live-captured in Long Island waters. Each bar indicates the percent of turtles in which the prey items occurred.

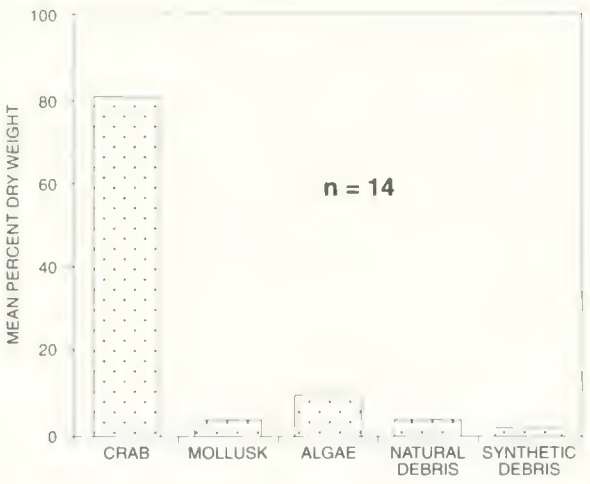

Figure 3

Mean percent of the fecal dry weight of general catergories of Kemp's ridley sea turtles (*Lepidochelys kempii*) prey items. Each area represents the mean percent of dry weight for that component of the feces (n=14). Crabs composed the predominant portion of the feces.

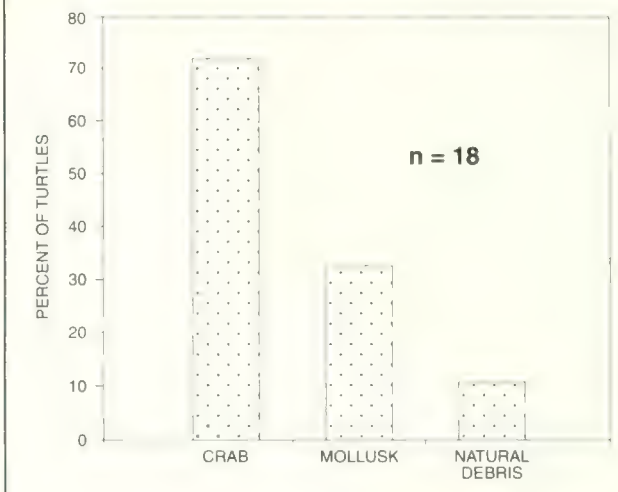

Figure 4

The percent of Kemp's ridley sea turtles (*Lepidochelys kempii*) from the digestive tract analysis that had consumed various types of ingesta. Most of the turtles had consumed crabs. Synthetics and algae were not present in the digestive tracts.

Included in three fecal samples were crab parts from which the fragments could not be identified to genus.

Mollusc species in the samples included blue mussels (*Mytilus edulis*) and bay scallops (*Argopectin irradians*). Two Kemp's ridley fecal samples contained mollusc fragments that could not be identified beyond phylum. Algal species in the samples included *Sargassum natans*, *Fucus* sp., and *Ulva* sp. A few turtles had small pieces of the macrophyte *Zostera marina* as well. Natural debris included such things as pebbles, small rocks, and bird feathers. Synthetic debris included only small pieces of polystyrene and latex.

Analysis of fecal components with dry weights (mean of percent per sample) revealed that crabs were the predominant component of all but one of the 14 fecal samples from 1989. The mean percent of crab dry weight for the samples was 80% (Fig. 3). The mean percent dry weight for each crab species revealed that spider crabs composed 60% of the identifiable crab parts. The remainder was composed of 22% rock crabs and 18% lady crabs. Thus, most of the Kemp's ridleys had consumed spider crabs, which represented a large portion of the bulk. Although more turtles consumed rock crabs than lady crabs, Kemp's ridleys that consumed lady crabs had feces composed exclusively of them.

For the period 1985 through 1989, 87 dead Kemp's ridleys were recovered from Long Island's waters. Gastrointestinal tracts were removed from 40 of the 87 turtles. Eighteen of the 40 stranded Kemp's ridleys contained identifiable diet components in the gut. All 18 turtles were juveniles. Mean straight-line carapace length for the 18 stranded turtles was 30.5 cm (range=24.8 cm to 39.7 cm, SD=3.5 cm). Thirteen of the 18 gastrointestinal tracks contained crab parts and seven contained mollusc shells (Fig. 4).

The most frequently encountered crabs in the gut content samples were spider crabs and rock crabs. Spider crab fragments were found in five of the 18 samples; rock crabs were found in four of the 18 samples. Lady crabs were found in two of the samples and the blue crab (*C. sapidus*) was found in the digestive tract of one Kemp's ridley. Two of the turtles had crab parts in their digestive tracts that could not be assigned reliably to any genus.

An additional 14 of the 40 Kemp's ridleys that were dissected had completely empty digestive tracts. All of these turtles had stranded from cold-stunning. Upon further review of necropsy data sheets from all of the Kemp's ridleys that had stranded during the study period, but from which samples were not preserved, it was noted that almost all of the cold-stunned individuals had empty or almost empty gastrointestinal tracts.

The remaining eight turtles had been collected in 1985 and 1986, and gut contents were unidentifiable because of improper preservation. These samples had been preserved for as long as five years prior to examination.

Discussion

The analysis of fecal samples from live turtles and of gut contents from dead specimens strongly suggests that crabs are the main dietary component for Kemp's ridleys in New York waters. Crab parts were present in 18 of the 19 turtles from which fecal samples were obtained and were the predominant food item by dry weight analysis. The analysis of fecal material, however, may be biased because it examines only that material which has not been fully digested. This could cause overrepresentation of less digestible components.

The gastrointestinal tract results (which are less susceptible to such bias) support the results of the fecal sample analysis. Of the 18 stranded turtles which contained identifiable food items, 13 contained crab parts in their guts. Gut contents can potentially be biased because of differential digestion. However, from our qualitative observation of the condition of the intestinal contents during dissection, we believe the components described herein are representative of the diet.

One difference between the fecal and intestinal samples was the source of the turtles. Most fecal samples were obtained from turtles captured in the Peconic Bays, but most stranded turtles were recovered on beaches adjacent to Long Island Sound. Presumably the dietary samples reflect feeding activities near the location of capture (or stranding). Thus, the observation of spider and rock crabs as the predominant components in the diets of both live-captured and stranded turtles emphasizes their importance as food items.

The dietary components observed during the study may be related to the relative abundance of the prey species in the environment. Of the four species of crab that were identified, the spider crab was both the most frequently encountered fecal component and the predominant crab identified in the gut contents of dead turtles. During the course of our studies we have noted that the nine-spined spider crab was one of the most common crabs in the waters where the turtles occurred. We have observed local commercial fishermen retrieving thousands of spider crabs while hauling in their nets. The Atlantic rock crab was also frequently encountered in the feces and gut contents of the turtles. The rock crab is also abundant in many of the areas in which the turtles occur.

Not all of the dietary make-up observed in this study can be explained by prey abundance. The green crab (*Carcinus maenus*) is very common in many of Long Island's estuaries but was not present in any of the turtles examined. This species usually inhabits shallower, rocky intertidal and subtidal habitats (Ropes, 1968; Williams, 1984), and our research on turtle behavior indicates that the Kemp's ridleys typically forage in deeper waters (Standora et al., 1990).

While we have commonly encountered lady crabs in the waters where turtles forage, this species was represented in only a few samples. Also rare in the samples was the locally and commercially harvested blue crab. Both the lady crab and the blue crab are portunid crabs, capable of swimming very quickly. This characteristic differentiates the portunids from the slower walking crabs, such as the spider and rock crabs.

The only molluscs consumed by turtles examined during this study included a few fragments of relatively thin-shelled blue mussels (*Mytilus edulis*) and bay scallops (*Argopectin irradians*), and entire shells of the small three-lined mud snail (*Nassarius trivitattus*). These mud snails are scavengers and can be found locally in association with dead fish and crabs (Long Island Shell Club, 1988). Their occurrence in four turtles, all of which had been cold-stunned, may indicate that the turtles were scavenging during periods of low water temperature.

Because sea turtles were obtained from different sources in New York waters, it was possible to obtain dietary information on a larger number of Kemp's ridleys. In many of the previous studies presented in Table 1, portunid crabs were indicated as a main dietary component for Kemp's ridleys. Although this crab family was observed in some New York turtles, it was of secondary importance to the walking crabs.

In terms of the overall life cycle of Kemp's ridleys, it appears that post-pelagic juveniles exploit the benthic environments of Long Island's estuaries, preying mainly on walking crabs. Data from our ongoing research indicate that sea turtles emigrating from New York inshore waters travel to southern coastal areas. Kemp's ridleys exhibiting this behavior may join the more southerly portion of the Atlantic population. Therefore, management plans for Kemp's ridleys should consider factors that affect benthic fauna, especially the abundant crab populations in the northeastern region. Such impacts could have far-reaching effects on a critical stage in the lives of these endangered sea turtles.

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Literature cited

Bellmund, S. A., J. A. Musick, R. C. Klinger, R. A. Byles, J. A. Keinath, and D. E. Barnard.
1987. Ecology of sea turtles in Virginia. Spec. Sci. Rep. No. 19, Virginia Institute of Marine Science, Coll. of William and Mary, Gloucester Point, Virginia.

Burke, V. J.
1990. Seasonal ecology of Kemp's ridley (*Lepidochelys kempi*) and loggerhead (*Caretta caretta*) sea turtles in the waters of Long Island, New York. Master's thesis, State University of New York, College at Buffalo, NY.

Burke, V. J., E. A. Standora, and S. J. Morreale.
1991. Factors affecting strandings of cold-stunned Kemp's ridley and loggerhead sea turtles in Long Island, New York. Copeia 1991:1136–1138.

Carr, A.
1942. Notes on sea turtles. Proc. New England Zoological Club 21:1–16.
1980. Some problems of sea turtle ecology. Am. Zool. 20:489–498.

DeSola, C. R., and F. Abrams.
1933. Testudinata from southeastern Georgia, including the Okefinokee swamp. Copeia 1:10–12.

Dobie, J. L., L. H. Ogren, and J. F. Fitzpartick Jr.
1961. Food notes and records of the Atlantic ridley turtle (*Lepidochelys kempii*) from Louisiana. Copeia. 1961:109–110.

Federal Register.
1989. Endangered and threatened wildlife and plants. 50 CFR 17.11 and 17.12.

Hardy, J. D.
1962. Comments on the Atlantic ridley turtle, *Lepidochelys olivacea kempi*, in the Chesapeake Bay. Chesapeake Science 3:217–220.

Liner, E. A.
1954. The herpetofauna of Lafayette, Terrebonne and Vermilion Parishes, Louisiana. Proc. Louisiana Academy of Sciences. 17:65–85.

Long Island Shell Club.
1988. Seashells of Long Island, New York. Long Island Shell Club, Inc., Long Island, NY.

Lutcavage, M.
1981. The status of marine turtles in Chesapeake Bay and Virginia coastal waters. Master's thesis, College of William and Mary, VA.

Marine Turtle Newsletter.
1989. IUCN resolution urges maximum size limits, protection of habitat, TED's. Mar. Turtle Newsletter. 44:1–3.

Pritchard, P. C. H., and R. Marquez.
1973. Kemp's ridley turtle or Atlantic ridley. International Union for the Conservation of Nature and Natural Resources Monograph No. 2, Marine Turtle Series. Morges, Switzerland.

Ropes, J. W.
1968. The feeding habits of the green crab, *Carcinus maenas* (L.). Fish. Bull. 67:183–200.

Schwartz, F. J.
1978. Behavioral and tolerance responses to cold water temperatures by three species of sea turtles (Reptilia, Cheloniidae) in North Carolina. Florida Marine Research Pub. 33:16–18.

Shaver, D. J.
1991. Feeding ecology of wild and head-started Kemp's ridley in South Texas waters. J. Herpetol. 25:327–334.

Standora, E. A., S. J. Morreale, E. Estes, R. Thompson, and M. Hilburger.
1989. Growth rates of Juvenile Kemp's ridleys and their movement in New York waters. Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology, p. 175–177.

Standora, E. A., S. J. Morreale, R. D. Thompson, and V. J. Burke.
1990. Telemetric monitoring of diving behavior and movements of juvenile Kemp's ridleys. Proceedings of the Tenth Annual Workshop on Sea Turtle Conservation and Biology, 133 p.

Williams, A. B.
1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C.

Zinn, D. J.
1984. Marine mollusks of Cape Cod. Cape Cod Museum of Natural History, Brewster, Massachusetts, 78 p.

Zug, G. R., and H. J. Kalb.
1989. Skeletochronological age estimates for juvenile *Lepidochelys kempi* from Atlantic coast of North America. Proceedings of the Ninth Annual Workshop on Sea Turtle.

Abstract.— The tripletail, *Lobotes surinamensis*, is the only member of the family Lobotidae in the western Atlantic Ocean, and its life history is poorly understood. We describe development of tripletail larvae, clarify the literature on their identification, and discuss their temporal and spatial distribution in the northern Gulf of Mexico. Larval tripletail are characterized by 1) a vaulted, median supraoccipital crest with spines along the leading edge; 2) precocious, heavily pigmented pelvic fins; and 3) large preopercular spines. In addition, the surface of the frontal and supraoccipital bones have a reticulated pattern of depressions or "waffled" appearance. Transition to juvenile stage begins at about 9.0-9.5 mm standard length. Tripletail have three supraneurals, six branchiostegal rays, 11 + 13 vertebrae, 27 dorsal rays (XII, 15), and 14–15 anal rays (III, 11–12). Overall, 75% of tripletail larvae were found in waters ≥28.8°C, ≥30.3 ppt, and at stations ≥70 m deep. Larval tripletail were collected primarily from July through September and almost exclusively in surface tows. Tripletail spawn offshore. Juveniles, although sporadic, are apparently not uncommon in Gulf of Mexico estuaries during summer.

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Larval development of tripletail, *Lobotes surinamensis* (Pisces: Lobotidae), and their spatial and temporal distribution in the northern Gulf of Mexico*

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The percoid family Lobotidae is usually considered to comprise two genera with about four species (Nelson, 1984), although Johnson (1984) only included *Lobotes*, questioning the affinity of *Datnioides*. The tripletail, *Lobotes surinamensis*, is cosmopolitan and found in all warm seas (Fischer, 1978); one adult was recorded as far north as St. Margarets Bay, Nova Scotia (44°37'N, 64°03'W (Gilhen and McAllister, 1985). *Lobotes surinamensis* is the only member of the family in the Gulf of Mexico (Gulf) (Hoese and Moore, 1977). Tripletail generally occur along the Gulf coast from April through early October (Baughman, 1941) and migrate south during fall and winter (Merriner and Foster, 1974). Although apparently abundant nowhere, adult and juvenile tripletail are not uncommon in bays, sounds, and estuaries along the north-central Gulf coast during summer (Baughman, 1941; Benson, 1982). Tripletail up to 18.6 kg and 89 cm standard length (SL) have been caught, but most average between 1 and 7 kg (Gudger, 1931; Baughman, 1941). Tripletail often are included as a category in Gulf fishing rodeos (Benson, 1982) because of their reputation as "a bold biter" and strong fighter (Gudger, 1931; Baughman, 1941). Tripletail enter the commercial catch on the east and west coasts of Florida and a few tons are taken annually (Fischer, 1978).

The development of tripletail larvae and their spatial and temporal distribution is poorly understood. Hardy (1978) compiled information on tripletail life history. Uchida et al. (1958) and Konishi (1988) provide limited information and illustrations of tripletail larvae off Japan; however, Konishi's 5.1–mm larva is misidentified. Johnson (1984) commented on cranial morphology. Our objectives were to describe the development of tripletail larvae, to clarify the literature on their identification, and to discuss the spatial and temporal distribution of larval tripletail in the northern Gulf of Mexico.

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Materials and methods

Tripletail larvae were obtained from museum collections throughout the Gulf of Mexico to determine their spatial and temporal distribution. These include collections from the Southeast Area Monitoring and Assessment Program's (SEAMAP) ichthyoplankton surveys of the Gulf from 1982 through 1986 (SEAMAP 1983–1987[1]); National Marine Fisheries Service (NMFS, Panama City, Florida) and Louisiana State University (LSU) collections from within riverine and oceanic frontal zones off the Mississippi River delta; and collections made by the Gulf Coast Research Lab (GCRL), Ocean Springs, Mississippi, and by Freeport-McMoRan Inc., New Orleans (Appendix Tables 1 and 2).

SEAMAP collections from 1982 to 1986 represent the first time-interval for which a complete set of data were available. Standard ichthyoplankton survey techniques as outlined by Smith and Richardson (1977) were employed in data collection. SEAMAP stations sampled by NMFS vessels were arranged in a systematic grid of about 55–km intervals. NMFS vessels primarily sampled waters >10 m deep. Each cooperating state had its own sampling grid and primarily sampled their coastal waters. Latitude 26°00'N was the southern boundary of the survey area. Hauls were continuous and made with a 60–cm bongo net (0.333-mm mesh) towed obliquely from within 5 m of the bottom or from a maximum depth of 200 m. A flowmeter was mounted in the mouth of each net to estimate volume of water filtered. Ship speed was about 0.75 m/sec; net retrieval was 20 m/min. At stations <95 m deep, tow retrieval was modified to extend a minimum of 10 minutes in clear water or 5 minutes in turbid water. Tows were made during both day and night depending on when the ship occupied the station. Overall, 1,823 bongo-net tows were collected and processed during these years. The SEAMAP effort from 1982 to 1984 also involved the collection and processing of 814 neuston samples taken with an unmetered 1×2 m net (0.947–mm mesh) towed at the surface for 10 minutes at each station. SEAMAP sampling during April and May was primarily beyond the continental shelf, whereas that during March and from June through December was over or immediately adjacent to the shelf at stations <180 m deep. No samples were taken during January and February. Additional information on the temporal and spatial coverage of SEAMAP plankton surveys is found in Stuntz et al. (1985), Thompson and Bane (1986, a and b), Thompson et al. (1988), and Sanders et al. (1990).

Collections from frontal zones off the Mississippi River delta include 311 surface-towed 1×2 m neuston net samples (0.333–mm mesh) made by NMFS. NMFS samples were collected during May, August, September, and December (1986 to 1989), although not all four months were sampled each year (Appendix Table 1). We also examined 63 surface-towed 1–m^2 Tucker trawl samples (0.363–mm mesh) taken at seven stations during July 1987, and 45 surface-towed multiple opening/closing net and environmental sensing system (MOCNESS) (Wiebe et al., 1976) samples (0.363–mm mesh) collected at five stations during April 1988. These samples were from LSU collections. In addition, we examined 17 samples from stations taken by LSU inside the 100-0m isobath during October 1990. The sampling area during October 1990 extended 140 km west from Southwest Pass of the Mississippi River delta along the inner-to mid-shelf. Samples were collected with a 60–cm bongo net (0.333–mm mesh) towed obliquely to the surface from 5 m of the bottom or from a maximum depth of 50 m (Appendix Tables 1 and 2).

Museum collections from GCRL and Freeport-McMoRan, Inc. were primarily taken off Mississippi Sound and within the Barataria Bay system of Louisiana, respectively. Gear type and most environmental data were not available from these two institutions (Appendix Table 2).

Temperature and salinity data were from the sea surface. Hydrographic data from stations where larvae were taken were multiplied by the total number of larvae collected at each station to derive median and mean hydrographic values. This method gives weight to distribution of larvae rather than to distribution of stations. We used percent cumulative frequency for defining the relationship between distribution of larval tripletail and water temperature, salinity, and station depth. Percent frequency indicates the range of hydrographic conditions most often associated with occurrences of tripletail larvae. Median, mean, and percent cumulative frequency statistics were calculated (SAS Institute, 1985).

An examination of tripletail larvae was made to describe developmental morphology. Body measurements were made on 21 tripletail between 2.2 and 23.0 mm SL (Table 1) according to the methods of Hubbs and Lagler (1958) and Richardson and Laroche (1979). Measurements were made to the nearest 0.1 mm with an ocular micrometer in a dissecting microscope. We follow Leis and Trnski's (1989) criteria for defining length of preopercular spines, body depth, head length, eye diameter, and

[1] SEAMAP. 1983–1987. (plankton). ASCII characters. Data for 1982–1986. Fisheries-independent survey data. National Marine Fisheries Service, Southeast Fisheries Center: Gulf States Marine Fish. Comm., Ocean Springs, unpubl. data.

Table 1

Morphometrics of larval tripletail (*Lobotes surinamensis*) from the northern Gulf of Mexico. Measurements are expressed as % standard length (SL).

SL	*n*	Preanal length	Head length	Snout length	Orbit diameter	Greatest body depth	Upper jaw length	Prepelvic distance
2.2–2.4	2	60.5–66.0	29.0–29.5	6.5–7.0	12.5–13.5	25.0–27.5	11.5–14.5	—
4.0–5.9	3	60.0–70.0	37.5–40.0	7.5–10.0	14.0–14.5	40.0–53.5	20.0–20.0	37.5–55.0
6.0–7.9	4	69.5–79.5	38.0–43.0	6.5–9.5	14.0–16.0	51.0–59.5	15.5–17.5	38.0–57.0
8.0–9.9	4	68.0–77.5	34.5–38.5	5.5–6.5	14.0–15.5	58.0–59.0	14.0–15.5	39.0–48.0
10.0–11.9	2	68.5–74.0	38.0–39.0	6.0–6.5	14.5–15.0	54.0–56.5	14.0–14.5	39.0–40.0
13.0–14.9	2	71.5–72.5	35.5–37.0	6.5–7.0	13.0–14.0	55.0–57.5	13.5–14.0	40.0–44.5
15.0–16.9	2	72.5–77.5	34.5–35.5	6.0–6.5	12.5–13.0	56.5–58.0	12.5–13.0	42.0–47.5
21.0–23.0	2	74.0–76.5	39.5–41.5	7.0–8.0	12.0–13.0	54.5–58.0	13.0–14.0	46.5–52.0

eye diameter/head length ratio. We consider notochord length in preflexion and flexion larvae synonymous with SL in postflexion larvae and report all lengths as SL unless otherwise noted. Specimens were fixed in 10% formalin and later transferred to 70% ethyl alcohol. Representative specimens were illustrated with the aid of a camera lucida. Because of the paucity of material, only two specimens were cleared with trypsin and stained with alizarin to examine head spines. We examined the surface of the occipital and frontal bones with a scanning electron microscope (SEM) after the epithelium was partially digested with trypsin. Soft rays of the dorsal and anal fins were counted when their pterygiophores were visible, and spines were counted when present.

Results

Larval morphometrics and pigmentation

Ninety-eight larval or juvenile tripletail were examined during this study (Appendix Table 2): 7 were preflexion or flexion (≤5.0 mm), 34 were postflexion (5.1 to 9.5 mm), and 57 were transforming or juvenile (>9.5 mm). Body depth increased rapidly during preflexion and flexion with depth >50% SL by 5.0 mm. The gut was straight. Larvae had 24 myomeres which became obscured by pigment in postflexion larvae. Preanal length was 60–65% SL in preflexion larvae and increased to 70–75% SL in larvae ≥5.0 mm. Head length averaged 29% SL during preflexion and increased to about 40% SL in juveniles. The head became increasingly steep, and the upper profile of the forehead was concave by 20.0 mm. The eye was large and had an orbit diameter usually from 35 to 40% head length (12.5 to 15.0% SL) by 4.0 mm. The upper jaw reached about mid-eye. Pelvic fins were precocious, heavily pigmented, and inserted behind the pectoral fins near mid-body, usually about 40–50% SL (Table 1). The pelvic fins extended past the anus by 4.0 mm.

Early preflexion larvae of 2.2–2.4 mm were sparsely pigmented; pigment was primarily restricted to the head and abdomen. On the head, external pigment was present on the posterior surface of the midbrain, posteriorly at the base of the supraoccipital crest, on the nape, and immediately anterior to the cleithral symphysis (Fig. 1). By early flexion (4.0 mm), pigment was added between the fore- and mid-brain and on the preopercle above the dorsal-most preopercular spine (Fig. 1). Pigment occurred at the tip of the upper and lower jaws and at the angle of the preopercle near the base of the angle spine by 5.0 mm. The head became heavily pigmented during postflexion. By 10.0 mm, a band of pigment extended diagonally across the head from the nape to the orbit and from below the orbit to the angle of the preopercle (Fig. 1). The eye was at the apex of this chevron-shaped band of pigment. Two parallel stripes of pigment were present between the orbits by 14.0–15.0 mm, extending from the nares to the anterior margin of the supraoccipital crest. These pigment stripes became better formed as larvae developed. On the abdomen, melanophores were distributed dorsally over the air bladder, and dorsally and ventrally along the visceral mass and hindgut of early larvae (Fig. 1). By early flexion, pigment also was present on the pectoral axilla, posteriorly over the visceral mass and hindgut, and was scattered laterally over the body above the visceral mass. Body pigmentation increased rapidly during early postflexion and extended posteriorly to the caudal peduncle by 6.0 mm (Fig. 1). Blotches or mottled areas of pigment formed over the body by 8.0–9.0 mm, becoming more evident as larvae developed (Fig. 1).

Pigment along the ventral midline between the anus and notochord tip was restricted to four to five

melanophores in early larvae. By early flexion, only one or two postanal melanophores were present along the ventral midline and these were located on the caudal peduncle and at the posterior margin of the hypural bones (Fig. 1). Pigment was also present on the developing pelvic fins by early flexion. Melanophores were distributed over the dorsal and anal spines by 6.0 mm and over the anterior-most dorsal and anal rays by 8.5–9.5 mm. Pigment covered all but the distal tips of the dorsal and anal rays by 15.0 mm. Only the base of the caudal- and pectoral-fin rays were pigmented by 13.0–14.0 mm (Fig. 1) and pigment covered about 50% of the caudal fin in a 23.0-mm larva. Pigment occurred only over the proximal portion of the dorsal-most pectoral-fin rays in the 23.0-mm larva.

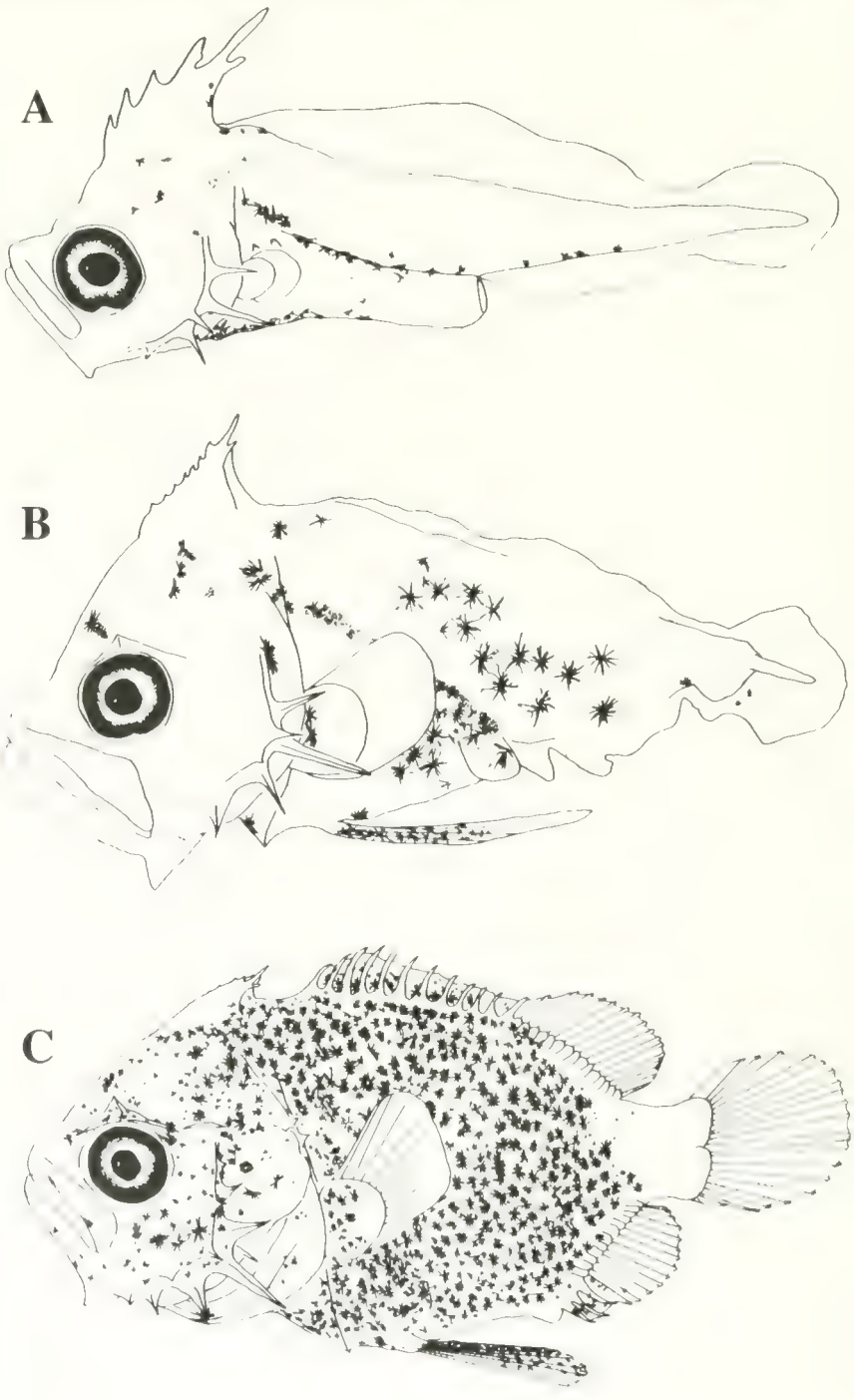

Figure 1

Larval development of tripletail (*Lobotes surinamensis*) from the northern Gulf of Mexico. (**A**) 2.2 mm, (**B**) 4.0 mm, (**C**) 6.3 mm, (**D**) 8.5 mm, (**E**) 10.8 mm, (**F**) 13.7 mm. All measurements are standard length (SL).

Head spination and fin development

Tripletail larvae were characterized by a vaulted, median supraoccipital crest, which originated above mid-eye, and by numerous spines and ridges on the head. Larvae of 2.2–2.4 mm had five to six spines along the leading edge of the supraoccipital crest and one spine on the posterior edge (Fig. 1). Usually eight spines occurred along the leading edge of the crest by 4.0 mm, giving the crest a serrate appearance. Length of the crest and its spines decreased as larvae grew (Fig. 1); and the entire supraoccipital crest was resorbed by 15.0–16.0 mm. The surface of the supraoccipital and frontal bones had a reticulated pattern of depressions or "waffled" appearance (Fig. 2). Because so few preflexion larvae were collected, we were unable to determine when this character first appeared. A large, laterally projecting supraorbital ridge with a single spine was present above the eye of tripletail larvae by 4.0 mm. Both the supraorbital spine and ridge were resorbed by 19.0 mm. Single, simple spines were present on the

posttemporal and supracleithrum by 4.5 mm; a low, simple ridge occurred along the pterotic at about 5.0 mm (Fig. 1). The posttemporal and supracleithral spines were partially covered by epithelium but both they and the pterotic ridge were visible on the largest specimen examined.

Tripletail larvae developed two series of preopercular spines, one along the outer shelf and the other along the inner shelf. Both outer and inner shelves have dorsal and ventral limbs. Three spines occurred along the posterior margin of the outer shelf of 2.2–2.4 mm larvae, the longest at its angle (Fig. 1). A fourth spine was forming but was small at 2.2 mm. Fifth and sixth spines were added by 6.0 mm; a seventh spine, by 7.0 mm. One to two small additional spines were added as larvae grew. By 15.5 mm, three to five spines were visible along the dorsal margin of the outer preopercular shelf, one at the angle, and usually three along the ventral margin; the anterior-most spine along the ventral margin was short and blunt (Fig. 1). All spines along the outer shelf were present in the largest specimen examined (i.e., 26.0 mm). Along the inner preopercular shelf, one spine was present in 2.2–2.4 mm larvae and three to four spines by 5.0 mm (Fig. 1). Spines along the inner shelf were short and blunt and covered by epithelium. A spine occurred along the posterior margin of the subopercle by 6.0–6.5 mm, near but dorsal to the angle spine of the outer preopercular shelf. The subopercular spine was resorbed by 20.0 mm. A small, flexible spine was present dorsally on the opercle by 10.0 mm. This spine was difficult to locate on unstained larvae because it was covered by integument.

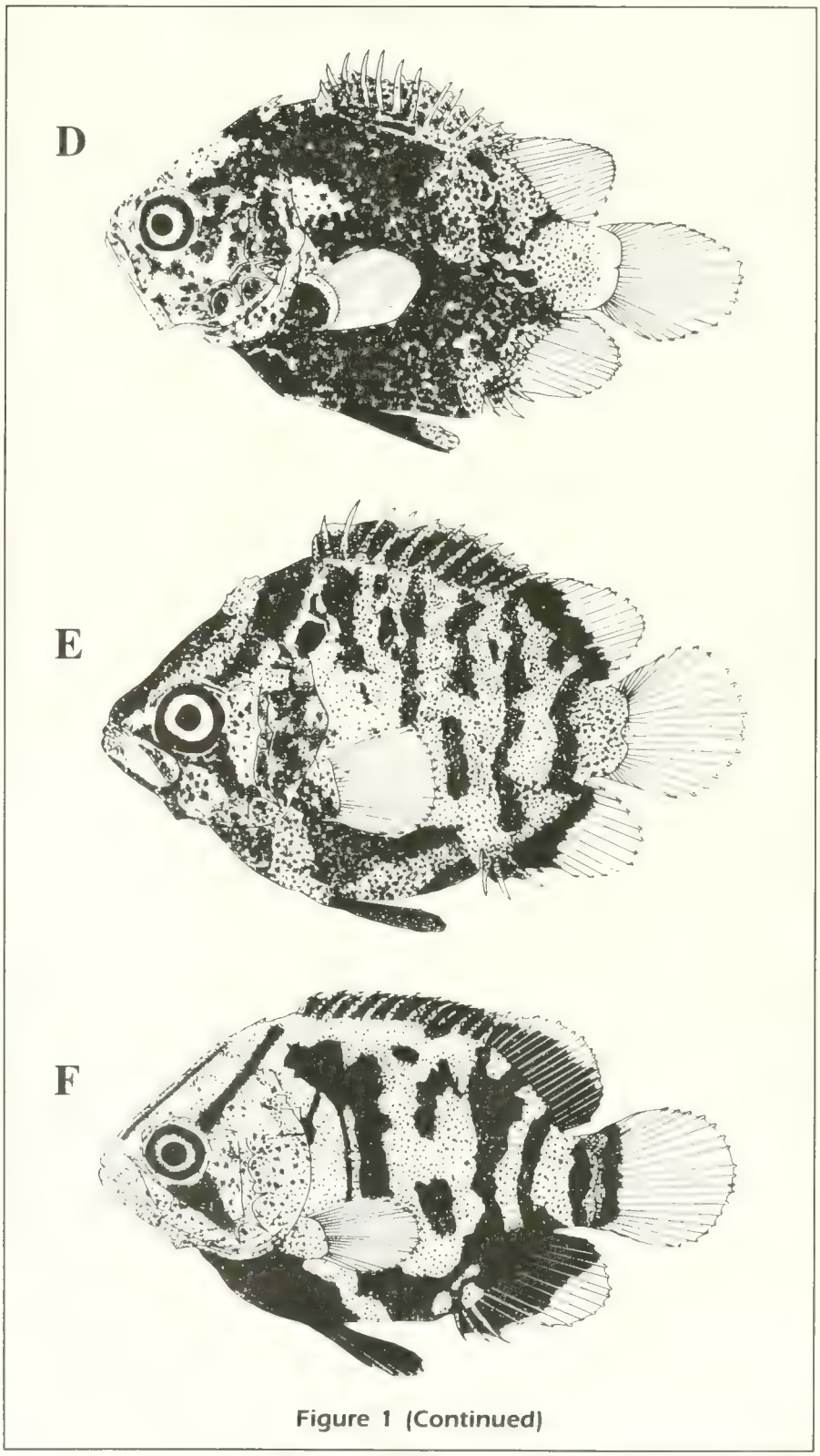

Figure 1 (Continued)

A continuous median finfold extended posteriorly around the body from the nape to the anus of early larvae. Pelvic fins were precocious and elongate (usually >25% SL) and had a full complement of

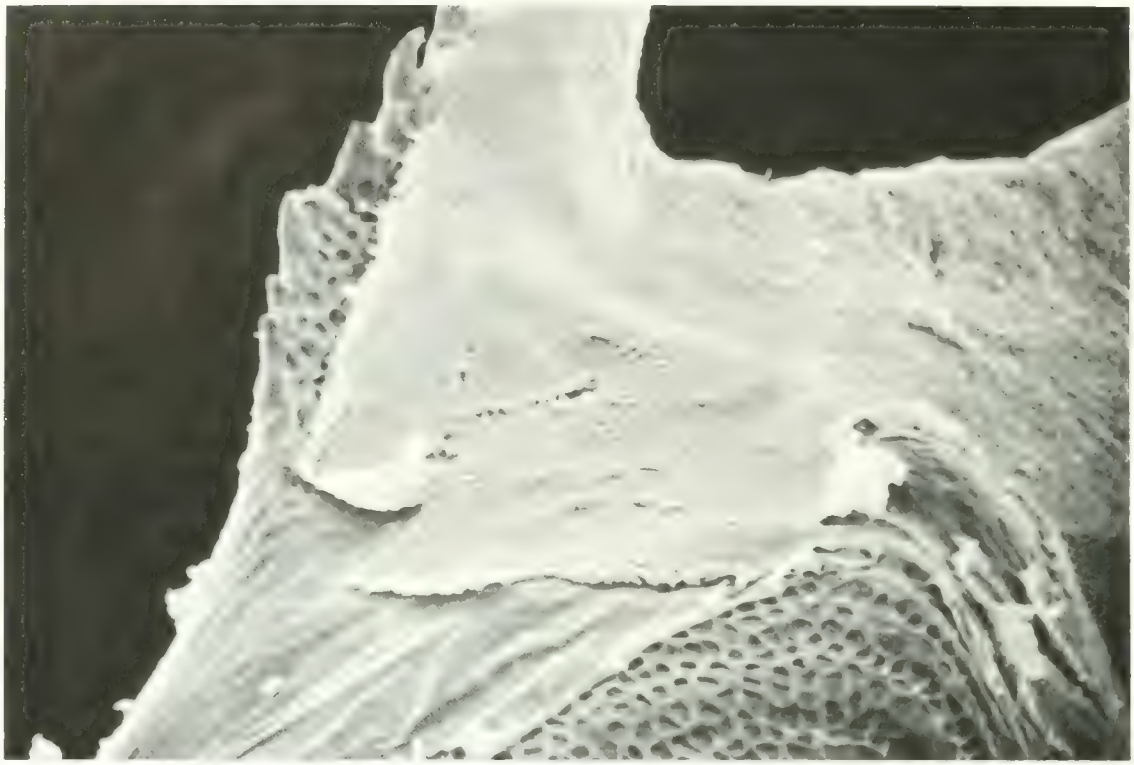

Figure 2

Scanning electron micrograph of the supraoccipital and frontal bones of a 6.3–mm standard length tripletail, *Lobotes surinamensis*, from the northern Gulf of Mexico. Magnification: 280×.

elements (I, 5) by 5.0 mm (Table 2). We were unable to determine when the pelvic-fin buds formed or flexion began because of a lack of specimens between 2.4 and 4.0 mm. Development of the hypural complex (by 4.0 mm) coincided with that of the pterygiophores of the dorsal and anal fins. Anlagen of caudal-fin rays formed obliquely in the caudal finfold. The central-most caudal-fin rays formed first and development proceeded outward from mid-base. Notochord flexion was complete by 5.0 mm. The adult complement of 9+8 principal caudal rays were present by 7.0 mm, as were all procurrent caudal rays by 9.0–9.5 mm. All dorsal- and anal-fin pterygiophores were present by 4.5–5.0 mm and both dorsal and anal spines developed before their rays in each fin. Dorsal and anal spines began to develop anteriorly and proceeded posteriorly to a full complement of elements in each fin by 6.5 mm. Pectoral rays began to form at 5.5–6.0 mm and a full complement (16 rays) was present by 7.0 mm (Table 2). A

Table 2

Fin ray counts of larval tripletail (*Lobotes surinamensis*) from the northern Gulf of Mexico. Measurements are in standard length (SL).

Size (mm SL)	*n*	Dorsal	Anal	Pectoral	Pelvic	Caudal
4.0	1	Finbase	Finbase	—	3	—
4.5	1	II, Anlagen	I, Anlagen	Anlagen	I, 5	4 + 3
5.0	1	VII, Anlagen	I, Anlagen	Anlagen	I, 5	6 + 6
6.3	1	XII, 15	II, 12	13	I, 5	7 + 7
7.1	1	XII, 15	III, 12	16	I, 5	3 – 9 + 8 – 2
10.2	1	XII, 15	III, 11	16	I, 5	4 – 9 + 8 – 4

cleared-and-stained 10.2–mm specimen had three supraneurals, six branchiostegal rays, four upper and four lower procurrent caudal rays, 11+13 vertebrae, 27 dorsal rays (XII, 15), and 14–15 anal rays (III, 11–12). Scales first appeared at 9.0–9.5 mm and marked the beginning of transition to the juvenile stage.

Spatial and temporal distribution

Overall, 75% of tripletail larvae in this study (Appendix Table 2) occurred at surface water temperatures ≥28.8°C (median=28.9°C, range=27.6–31.0°C), at salinities ≥30.3 ppt (median=31.3 ppt, range=22.0–36.0 ppt), and at stations ≥70 m deep (median=205 m, range=1–2707 m) (Figs. 3 and 4). Larvae <5.0 mm were collected only at stations ≥110 m deep. The two smallest larvae (2.2 and 2.4 mm) were taken on 28 July 1987 in a Tucker trawl sample at a station 110 m deep off Southwest Pass of the Mississippi River (Appendix Table 2). Other life stages were collected throughout the study area (Fig. 5, Appendix Table 2).

Tripletail larvae were taken almost exclusively from July through September. Two specimens were collected in neuston nets outside this time period, one taken on 21 May 1983 (7.0 mm) and the other by GCRL on 9 October 1968 (10.2 mm) (Appendix Table 2). Salinity (36.5 ppt) and station depth (2,707 m) for the May specimen were the maximums recorded for a station where larvae were collected during this study (Appendix Table 2).

Larval tripletail were collected primarily near the surface. Only 2 of 528 oblique bongo-net collections between July and September yielded tripletail larvae (n=6, 6.0–9.0 mm, 18 September 1985). Of 537 total surface net tows taken during this same time period, only 31 tows (5.8%) collected tripletail lar-

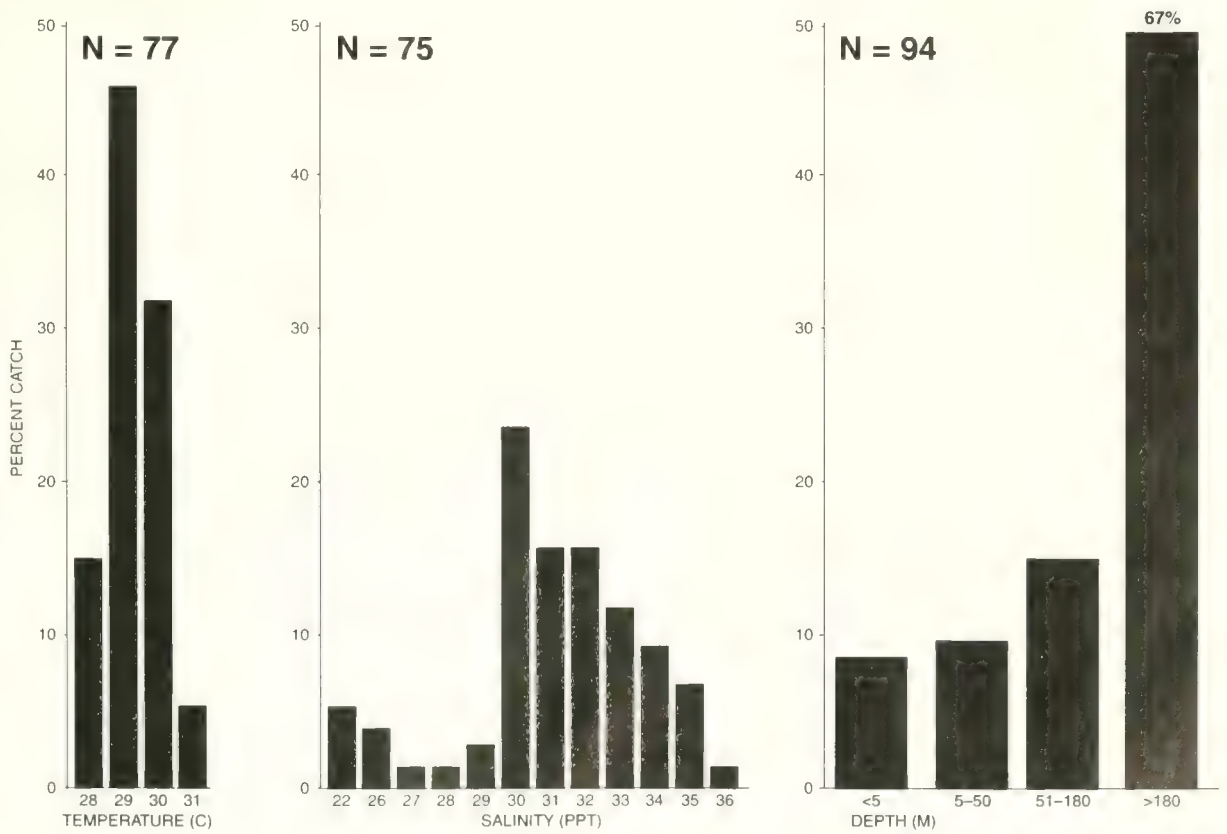

Figure 3

Summary of hydrographic data from positive catch stations for larval tripletail (*Lobotes surinamensis*) in the northern Gulf of Mexico. Percent catch is sum of larvae by interval divided by total number of tripletail larvae collected overall. Discrepancies in n (number of larvae), among parameters, are the result of missing hydrographic data. Depth is station depth.

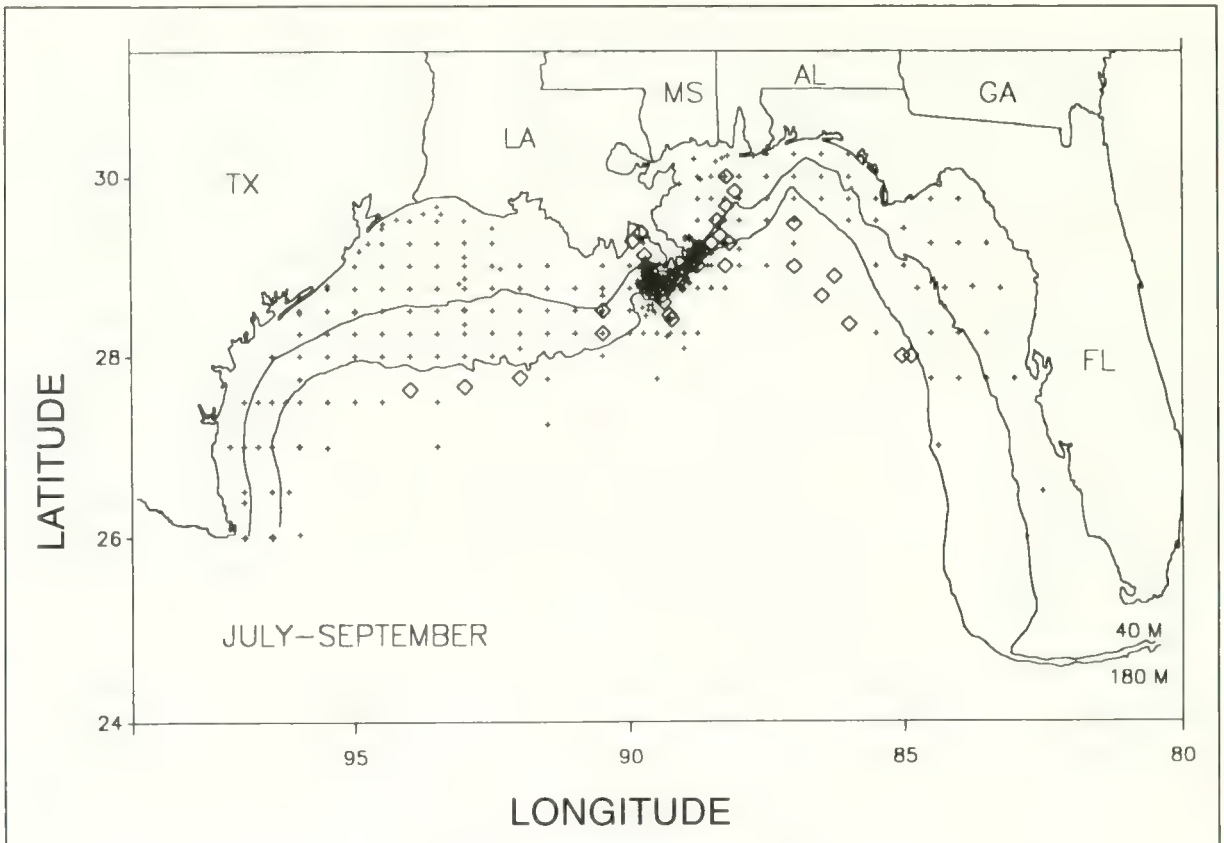

Figure 4

Distribution of larval tripletail (*Lobotes surinamensis*) in the northern Gulf of Mexico. Plus (+) signs are stations sampled; open diamonds are positive catch stations. Data are for collections between July and September 1966–89.

vae (n=79) (Appendix Tables 1 and 2). Larvae from GCRL and Freeport-McMoRan collections also occurred primarily between July and September, but collection data are not available (e.g., total number of stations sampled and extent of sampling area).

Discussion

The developmental morphology of tripletail larvae from the Gulf generally agrees with limited information provided by Uchida et al. (1958) and Johnson (1984). Larval tripletail are characterized by 1) a vaulted, median supraoccipital crest with spines along the leading edge; 2) precocious, heavily pigmented pelvic fins; and 3) large preopercular spines (Uchida et al., 1958; Johnson, 1984; this study). The supraoccipital crest is resorbed by 15.0–16.0 mm SL in Gulf specimens (this study) and by 17.5 mm TL (probably about 16.0 mm SL) off Japan (Uchida et al., 1958). Johnson (1984) described the surface of the frontal and supraoccipital bones of tripletail larvae as rugose. We would characterize these bones as having a "waffled" appearance rather than an elevated one, as implied by rugose (Fig. 2). Regardless, this modification is found in relatively few other taxa (Johnson, 1984). Sequence of fin completion in larval tripletail is P_2–D_1–D_2–A-P_1 and is unlike the six patterns described by Johnson (1984). The third anal spine is the last dorsal- or anal-fin element to form. The dark band of pigment extending backward from above and below the orbit in 10.0–mm larvae is present at 8.3 mm SL (10.6 mm TL) off Japan (Uchida et al., 1958) and in juveniles and adults (Gudger, 1931; Breder, 1949). We did not find the nasal spine noted by Uchida et al. (1958). The 5.1–mm TL specimen listed as *L. surinamensis* by Konishi (1988) lacks a supraoccipital crest and precocious pelvics, and it has a small, multi-serrate supraorbital ridge rather than the single supraorbital spine we found. Thus, we believe that Konishi's 5.1–mm TL specimen is not *L. surinamensis*.

Because tripletail have a cosmopolitan distribution, their larvae may be confused with many taxa. Larval tripletail resemble larvae of caproids, some carangids, cepolids, drepaneids, ephippids, leiog-

nathids, lethrinids, priacanthids, and *Hapalogenys* sp. These taxa generally have a median supraoccipital crest, an elongate spine at the preopercular angle, and about 24 myomeres (except cepolids which have 28+ myomeres). In addition, cepolids are lightly to moderately pigmented and have fewer dorsal spines and more soft dorsal-fin rays than tripletail (Leis and Trnski, 1989). Species of other families may have a median supraoccipital crest during development, but most have pelvic fins inserted anterior to pectorals. Also, larvae of other percoid families are usually not as deep-bodied and as heavily pigmented as tripletail by early postflexion, and few possess an elongate preopercular spine and low myomere count. Of the aforementioned taxa, only caproids, carangids, ephippids, and priacanthids occur in the Gulf of Mexico. Larvae of the caproid genus *Antigonia* are most similar to tripletail but have a serrate frontal crest and lower jaw, a very long and serrate preopercular angle spine, and more than 39 dorsal and 26 anal elements (Tighe and Keene, 1984; Leis and Trnski, 1989). In carangids, the two anterior-most anal spines are separated from the third by a distinct gap and most species have a low, median supraoccipital crest with dorsal serrations; other carangids lack a supraoccipital crest entirely. Some carangids also have a precocious dorsal fin with elongate anterior spines or rays, or a serrated preopercular angle spine. Drepaneids have pigment on the pectoral fins and multiple barbels along the lower jaw. Both larval drepaneids and ephippids are rotund and have pelvic fins inserted anterior to the pectorals. In addition, the Gulf ephippid *Chaetodipterus faber* has a supraoccipital crest with a single spine dorsally rather than the vaulted, serrate supraoccipital crest found in tripletail. Atlantic spadefish also have more anal fin elements (tripletail: A. III, 11–12; Atlantic spadefish: A. III, 17–18). Larval leiognathids and lethrinids have a supraoccipital crest that originates above the anterior margin of the eye and both taxa are lightly pigmented (Leis and Trnski, 1989). Also, lethrinids have higher anal fin counts and serrations along the lower jaw (Leis and Rennis, 1983), and leiognathids have a distinctive pattern of pigment ventrally on the tail (Leis and Trnski, 1989). Priacanthids have serrate dorsal, anal, and pelvic spines and other serrate ridges and spines on the head that tripletail lack (Johnson, 1984). *Hapalogenys* sp. larvae are extremely similar to tripletail but *Hapalogenys* sp. apparently lack pigmented pelvic fins, have a serrate supraorbital ridge, have a lacrimal spine, and have pterotic spines or a ridge (Johnson, 1984).

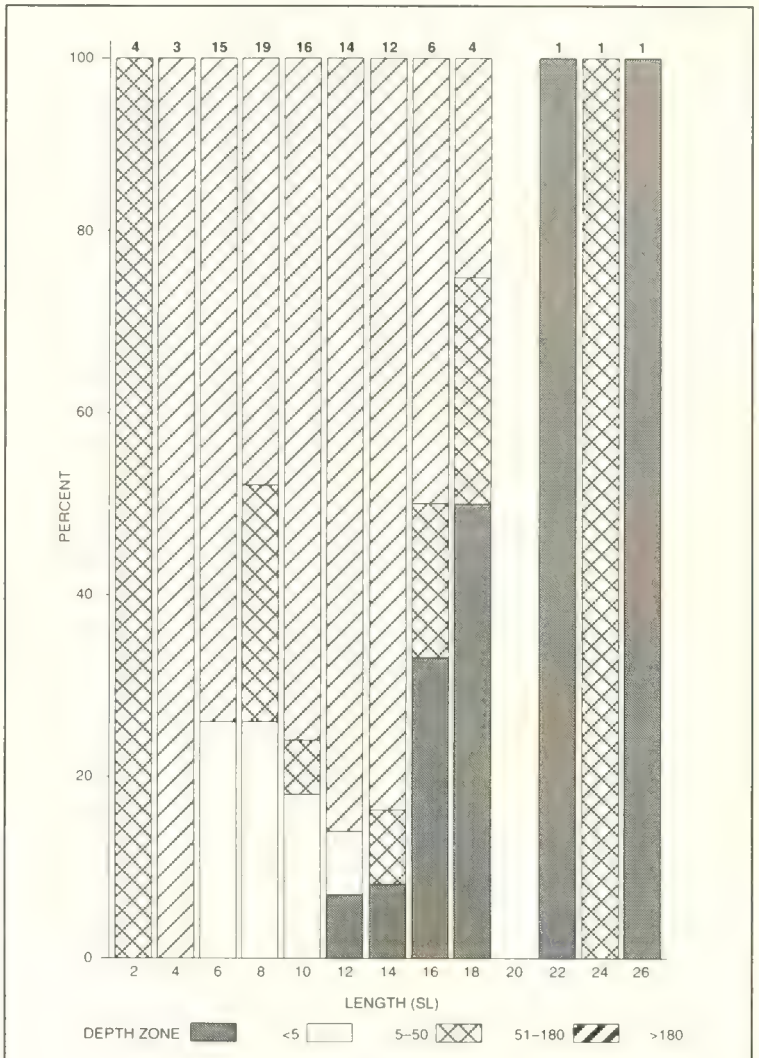

Figure 5

Distribution of larval tripletail (*Lobotes surinamensis*) in the northern Gulf of Mexico with respect to station depth (m). Length classes are combined as follows: 2 mm = 1.0–2.9 mm, 4 mm = 3.0–4.9 mm, 6 mm = 5.0–6.9 mm, etc. All measurements are standard length (SL). Numbers above bars are number of larvae in each length category.

Collections of early larvae (this study) and gravid females (Baughman, 1941; Merriner and Foster, 1974) suggest that tripletail spawn primarily during summer along both the U. S. Gulf and Atlantic coasts. In the Gulf, spawning begins in May, based on the collection of a 7.0–mm larva, and extends through September with peak spawning during July

and August (Appendix Table 2). These findings support Baughman's (1941) observation that eggs in gravid females are largest during July and August and small or absent thereafter. Larvae are collected primarily during August and September off Japan (Uchida et al., 1958).

Tripletail spawn offshore. This hypothesis of offshore spawning is supported by the collection of all larvae <5.0 mm at stations on the outer shelf and in oceanic waters. We found no published information on larval distribution as related to water temperature, salinity, or station depth of capture.

Larval and juvenile tripletail are collected primarily in surface tows (Uchida et al., 1958; this study). Juveniles are often collected with drifting sea weeds, including *Sargassum*, and near floating objects (Baughman, 1943; Breder, 1949; Uchida et al., 1958; Dooley, 1972; Benson, 1982) as they float on their side (Gudger, 1931; Breder, 1949). The size at which tripletail become associated with drifting sea weeds is poorly known, but Uchida et al. (1958) collected juveniles between 10.0 and 20.0 mm TL in seaweeds.

Adult tripletail occur primarily in gulf waters, but enter passes, inlets, and bays near river mouths (Gudger, 1931; Baughman, 1941). The degree to which tripletail utilize estuaries during their life history is unknown. Juveniles are apparently not uncommon (although they may be sporadic) in Gulf coast estuaries during the summer. We examined eight specimens (14.5–26.0 mm) collected at the surface in waters ≤3 m deep (Fig. 5). Modde and Ross (1981) collected 236 juvenile tripletail (size range not given) during 1976 in the surf zone of Horn Island, Mississippi, but only one during 1975 and five during 1977. Juveniles also occur in shallow waters (1–3 m) within the Barataria Bay system of Louisiana.[2] In contrast, juvenile and adult tripletail in the Indian River lagoon off the east coast of Florida occupy areas which average 30–31 ppt. The lagoon typically goes hypersaline, to 40 ppt, during spring when most tripletails first appear in the lagoon. Tripletail have not been observed or captured in extensive collections of oligohaline areas of the St. Lucie River and Sebastian Creek.[3]

Adult tripletail generally occur along the Gulf coast from April through early October (Baughman, 1941) and are caught in great numbers in Mobile Bay, Alabama, and along the Mississippi coast during summer (Baughman, 1941). Greatest concentrations of adults are found along the northern Gulf from St. Marks, Florida, to the St. Bernard River, Texas (Baughman, 1941). Seasonality of adults suggests that tripletail migrate south during fall and winter and return in spring (Merriner and Foster, 1974). Tripletail congregate around sea buoys, beacons, pilings, and other objects (Gudger, 1931) but have been collected in a wide variety of habitats including rocky and coral reef areas in deeper water (Baughman, 1941).

[2] Leroy Kennair, Freeport-McMoRan, Inc., New Orleans, LA., pers. commun. 1993.

[3] R. Grant Gilmore, Harbor Branch Oceanographic Institution, Fort Pierce, FL, pers. commun. 1993.

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Literature cited

Baughman, J. L.

1941. On the occurrence in the Gulf coast waters of the United States of the triple tail, *Lobotes surinamensis*, with notes on its natural history. Am. Nat. 75:569–579.

1943. Additional notes on the occurrence and natural history of the triple tail, *Lobotes surinamensis*. Am. Midl. Nat. 29(2):365–370.

Benson, N. G. (ed.).

1982. Life history requirements of selected finfish and shellfish in Mississippi Sound and adjacent areas. U.S. Fish and Wildl. Serv., Office Biol. Serv., Washington, D.C., FWS/OBS-81/51, 97 p.

Breder, C. M., Jr.

1949. On the behavior of young *Lobotes surinamensis*. Copeia 1949(4):237–242.

Dooley, J. K.

1972. Fishes associated with the pelagic sargassum complex, with a discussion of the sargassum community. Contrib. Mar. Sci., Univ. Texas 16:1–32.

Fischer, W., (ed.).
1978. FAO species identification sheets for fishery purposes. Western Central Atlantic (Fishing Area 31), Vol. 3. FAO, Rome.

Gilhen, J., and D. E. McAllister.
1985. The tripletail, *Lobotes surinamensis*, new to the fish fauna of the Atlantic coast of Nova Scotia and Canada. Can. Field-Natur. 99(1):116–118.

Gudger, E. W.
1931. The tripletail, *Lobotes surinamensis*, its names, occurrence on our coasts and its natural history. Am. Nat. 65: 49–69.

Hardy, J. D., Jr.
1978. Development of fishes of the Mid-Atlantic Bight: an atlas of egg, larval and juvenile stages. Vol. III: Aphredoderidae through Rachycentridae. U.S. Fish. Wildl. Serv., Biol. Serv. Prog. FWS/OBS-78/12.

Hoese, H. D., and R. H. Moore.
1977. Fishes of the Gulf of Mexico: Texas, Louisiana, and adjacent waters. Texas A&M Univ. Press, College Station, 327 p.

Hubbs, C. L., and K. F. Lagler.
1958. The fishes of the Great Lakes region. Univ. Mich. Press, Ann Arbor, 213 p.

Johnson, G. D.
1984. Percoidei: development and relationships. *In* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson (eds.), Ontogeny and systematics of fishes, p. 464–498. Am. Soc. Ichthy. Herp., Spec. Publ. No. 1.

Konishi, Y.
1988. Lobotidae. *In* M. Okiyama (ed.), An atlas of the early stage fishes in Japan. Tokai Univ. Press, Tokyo, 1,154 p. (In Japanese.)

Leis, J. M., and D. S. Rennis.
1983. The larvae of Indo-Pacific coral reef fishes. Univ. Hawaii Press, Honolulu, 269 p.

Leis, J. M., and T. Trnski.
1989. The larvae of Indo-Pacific shorefishes. Univ. Hawaii Press, Honolulu, 371 p.

Merriner, J. V., and W. A. Foster.
1974. Life history aspects of the tripletail, *Lobotes surinamensis* (Chordata-Pisces-Lobotidae), in North Carolina waters. J. Elisha Mitchell Sci. Soc. 90(4):121–124.

Modde, T., and S. T. Ross.
1981. Seasonality of fishes occupying a surf zone habitat in the northern Gulf of Mexico. Fish. Bull. 78(4):911–922.

Nelson, J. S.
1984. Fishes of the World. 1984, 2nd ed. John Wiley & Sons, NY, 523 p.

Richardson, S. L., and W. A. Laroche.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (Family Scorpaenidae) off Oregon. Fish. Bull. 77(1):1–46.

Sanders, N., Jr., T. Van Devender, and P. A. Thompson.
1990. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1986. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 20, 328 p.

SAS Institute, Inc.
1985. SAS user's guide: statistics, 1985 ed. SAS Institute, Cary, NC, 584 p.

Smith, P. E., and S. L. Richardson.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Paper No. 175, 100 p.

Stuntz, W. E., C. E. Bryan, K. Savastano, R. S. Waller, and P. A. Thompson.
1985. SEAMAP environmental and biologcial atlas of the Gulf of Mexico, 1982. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 12, 145 p.

Thompson, P. A., and N. Bane.
1986a. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1983. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 13, 179 p.
1986b. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1984. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 15, 171 p.

Thompson, P. A., T. Van Devender, and N. J. Sanders, Jr.
1988. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1985. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 17, 338 p.

Tighe, K. A., and M. J. Keene.
1984. Zeiformes: development and relationships, p. 393–398. *In* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson (eds.), Ontogeny and systematics of fishes. Am. Soc. Ichthy. Herp., Spec. Publ. No. 1.

Uchida, K., S. Imai, S. Mito, S. Fujita, M. Ueno, Y. Shojima, T. Senta, M. Tahuka, and Y. Dotsu.
1958. Studies on the eggs, larvae, and juveniles of Japanese fishes. Series 1: Second lab. of fish. biol. Fish. Dep., Fac. Agric., Kyushu Univ., Fukuoka, Japan.

Wiebe, P. H., K. H. Burt, S. H. Boyd, and A. W. Morton.
1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. J. Mar. Res. 34(3):313–326.

Appendix Table 1

Summary of total number of bongo-net/neuston-net stations examined for tripletail larvae (*Lobotes surinamensis*) in the Gulf of Mexico. Acronyms are as follows: SEAMAP = Southeast Area Monitoring and Assessment Program; NMFS = National Marine Fisheries Service, Panama City, Florida; LSU = Louisiana State University. NS means no samples.

	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
SEAMAP										
1982	77[1]/0[2]	69/68	71/73	102/100	26/24	NS	NS	3/8	29/3	NS
1983	15/13	27/27	84/84	55/45	44/42	NS	NS	39/26	NS	24/23
1984	23/0	44/0	46/0	55/54	20/26	155/162	NS	24/0	6/0	36/36
1985	29/0	NS	NS	85/0	39/0	69/0	20/0	4/0	2/0	24/0
1986	NS	24/0	90/0	57/0	10/0	NS	145/0	43/0	73/0	24/0
TOTAL	144/13	164/95	291/157	354/199	139/92	224/162	165/0	113/34	110/3	108/59
NMFS[2]										
1986							46			
1987							68			
1988			55			71				36
1989							35			
LSU										
1987[3]					63					
1988[4]		45								
1990[1]								17		

[1] 60-cm bongo net, 0.333-mm mesh, oblique-tow from depth.
[2] 1 × 2 m neuston net, 0.947-mm mesh, 10 min. surface-tow, unmetered.
[3] 1m^2 Tucker trawl, 0.947-mm mesh, 3 min. surface-tow each net, nine net collections per station, seven total stations.
[4] 1m^2 MOCNESS, nine nets of 0.333-mm mesh, 3-min. surface-tow each net, five total stations.

Appendix Table 2

Positive catch station data for tripletail (*Lobotes surinamensis*) larvae from northern Gulf of Mexico waters. Gear codes are: B=bongo net, N=Neuston net, T=Tucker trawl, U=unknown.

Station	Date	Gear	Latitude	Longitude	Station depth (m)	°C	PPT	*n*	Length (mm SL)
SEAMAP[1]									
1420	5–21–83	N	26°30	88°00	2707	27.6	36.5	1	7.0
3235	7–17–84	N	28°15	90°30	70	29.4	25.9	1	8.8
3238	7–17–84	N	28°30	90°30	38	29.4	25.8	1	7.0
3259	7–22–84	N	29°00	87°00	1251	28.9	32.8	1	12.3
2511	8–03–84	N	29°00	88°15	1013	27.6	32.4	7	7.1–18.5
2523	8–03–84	N	29°15	88°30	82	28.0	26.0	1	7.9
2548	8–05–84	N	29°00	88°45	249	27.6	28.7	1	16.8
4231	8–05–84	N	29°28	87°00	486	28.9	30.3	16	6.8–13.0
4201	8–01–85	N	28°00	84°52	205	29.6	30.8	10	10.3–15.9
4204	8–01–85	N	28°00	85°02	265	28.8	32.6	5	9.0–16.5
4210	8–02–85	N	28°21	86°00	457	28.8	32.1	4	6.8–10.0
4216	8–03–85	N	28°53	86°16	335	29.1	31.3	2	9.0
4219	8–03–85	N	28°40	86°30	457	28.9	33.6	1	9.9
4320	8–24–85	N	27°38	94°00	455	28.0	—	1	4.0
4326	8–25–85	N	27°40	93°00	265	29.7	36.0	1	7.8
4332	8–26–85	N	27°46	92°00	457	30.0	35.4	1	9.1
4484	9–18–85	B	29°07	89°44	20	27.8	29.5	2	6.0
4490	9–18–85	B	28°37	90°26	27	27.8	32.6	4	6.4–9.0
LSU[2]									
137	7–28–87	T	28°42	89°29	110	29.5	22.0	2	2.2–2.4
145	7–28–87	T	28°35	89°22	182	29.6	32.5	2	5.0
163	7–30–87	T	28°24	89°14	640	31.0	33.6	2	6.3
168	7–30–87	T	28°24	89°14	640	31.0	33.6	2	6.3
175	7–30–87	T	28°27	89°16	410	29.8	35.3	2	—
177	7–30–87	T	28°27	89°16	410	29.8	35.3	2	4.5
GCRL[3]									
Station 6	7–13–67	N	29°15	88°11	182	—	—	1	12.5
T–108–7–02	8–25–71	U	29°10	88°45	55	—	—	1	8.7
T–108–3–04	8–27–71	U	29°50	88°05	27	—	—	1	11.7
T–208–4–01	8–23–72	U	29°40	88°14	38	—	—	2	7.2–7.3
T–109–6–02	9–21–71	U	29°20	88°21	55	-	—	1	15.4
T–109–5–03	9–22–71	U	29°30	88°24	46	—	—	1	8.6
T–209–2–01	9–15–72	U	30°00	88°14	27	—	—	2	7.7–10.7
Station 5	10–09–68	N	29°19	88°14	73	—	—	1	10.2
Freeport-McMoRan[4]									
2	8–24–71	U	29°16	89°57	1	—	—	1	14.5
3	8–10–71	U	29°22	89°48	3	—	—	2	16.5–18.5
4	8–23–73	U	29°16	89°57	1	—	—	1	26.0
5	8–15–66	U	29°16	89°57	3	—	—	4	11.5–21.5
NMFS[5]									
53	8–28–88	N	29°00	88°53	149	30.3	27.5	1	10.8
58	8–29–88	N	29°07	88°49	82	29.5	29.0	1	13.7
5	9–03–87	N	29°12	88°43	71	29.3	32.8	1	23.0
23	9–25–86	N	28°50	89°05	195	29.4	34.0	2	7.3–13.2
32	9–06–89	N	28°49	89°16	410	29.8	35.3	1	18.7
42	9–26–86	N	29°09	88°40	77	29.3	—	1	8.6
43	9–05–87	N	28°46	89°29	104	29.2	32.1	1	7.5

[1] Southeast Area Monitoring and Assessment Program.
[2] Louisiana State University, Coastal Fisheries Institute, Baton Rouge.
[3] Gulf Coast Research Lab, Ocean Springs, Mississippi.
[4] Freeport-McMoRan, Inc., New Orleans, Louisiana.
[5] National Marine Fisheries Service, Panama City Lab, Florida.

Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus*, (Lacepede 1802) from Lizard Island, Northern Great Barrier Reef

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Abstract.— Otoliths were used to determine the age and growth of the coral trout *Plectropomus leopardus* from Lizard Island area, Northern Great Barrier Reef, Australia. An alternating pattern of opaque (annulus) and translucent zones was visible in whole and sectioned otoliths. However, compared to sectioned otoliths, whole readings tended to underestimate age of older fish. Otoliths of mark-recaptured fishes treated with tetracycline showed that one annulus is formed per year during the winter and spring. The oldest individual examined was 14 years of age. Schnute's growth formula was used to determine the best model to describe the growth of the coral trout. The von Bertalanffy model for fork length (FL) fitted the data well and the resulting model was $L_t = 52.2\,(1 - e^{-0.354(t + 0.766)})$. Line-fishing usually does not capture fishes smaller than 25 cm FL, thereby excluding most 0+ and 1+ year old fish and probably the slower growing 2+ year old fish. These first three years of life represent the period of fastest growth, so, if the growth curve is fitted only to the line fishing data, the growth rate of the population is underestimated. Multiple regression was used to predict age from otolith weight and fish length and weight. Otolith weight was the best predictor of age in the linear model and explained as much variation in age as fish size in the von Bertalanffy model.

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The coral trouts of the genus *Plectropomus* Oken are members of the serranid subfamily Epinephelinae, commonly known as groupers. These fishes occur in shallow tropical and subtropical seas of the Indo-Pacific region (Randall and Hoese, 1986) where they usually are at the top of food chains and thus play a major role in the structure of coral reef communities (Randall, 1987).

Groupers typically represent an important fishery resource throughout the tropical and subtropical regions of the world (Ralston, 1987). On the Great Barrier Reef, the common coral trout *Plectropomus leopardus* (Lacepede 1802) is the most abundant species of the genus (Randall and Hoese, 1986) and usually the primary target of recreational and commercial fishermen. The Queensland commercial line-fishing fleet takes a total annual catch of about 4,000 metric tons (t) of reef and pelagic species. The coral trout composes the largest single component of this catch (over 30%) with around 1200 t caught annually (Trainor, 1991). The recreational sector of this fishery is estimated to catch two to three times the commercial catch of reef fish (Craik, 1989[1]).

Worldwide studies on age and growth of Epinephelinae indicate that they are long lived, slow growing, and have relatively low rates of natural mortality (Manooch, 1987). Fishes with these characteristics are susceptible to overfishing. Only by obtaining validated estimates of growth is it possible to determine population dynamics, estimate potential yield, monitor the responses of populations to fishing pressure, and properly manage the fishery.

Some information on age, growth, and longevity is available for the common coral trout. On the Great Barrier Reef, Goeden (1978) estimated the growth rate of this species at Heron Island from length-frequency data. Mcpherson et al. (1988), determined age and growth of the common coral trout in the Cairns region by counts of annuli in whole otoliths. Loubens (1980) estimated age and growth for *P. leopardus* from New Caledonia from counts of annuli in broken and burnt otoliths. The periodicity of formation of annual rings in the latter two studies was verified through observation of marginal

[1] Craik, G. J. S. 1989. Management of recreational fishing in the Great Barrier Reef Marine Park Tech. Memo. GBRMPA-TM-23, 35p.

increments in otoliths. Direct validation of age has not yet been attempted for *P. leopardus*.

Fish population models usually require a general description of the growth process by means of an appropriate mathematical function. The von Bertalanffy (1938) growth model is the most studied and the most frequently used, since its application by Beverton and Holt (1957) to the yield-per-recruit problem (Kimura, 1980; Gallucci and Quinn, 1979). Many alternative growth curves have been proposed (see Moreau, 1987) as well as the use of polynomial functions (Chen et al., 1992). In this work, Schnute's (1981) formula was used to find the model that best described the growth of *P. leopardus*.

For several species of fishes, otolith growth has been found to continue with age, independent of fish size (Boehlert, 1985; Casselman, 1990; Beckman et al., 1991). Boehlert (1985) suggested the use of otolith weight as a non-subjective, cost-effective methodology for age determination that would decrease variability among age estimates.

The aims of this study were to obtain direct validation of age-at-length information and to find the model that best described the growth of the common coral trout from Lizard Island, Northern Great Barrier Reef, Australia. In addition, the relationship between otolith weight, body size, and age of the coral trout was studied to understand the mode of growth of the otolith and to assess the usefulness of otolith dimensions in predicting age.

Materials and methods

Coral trout (n=310) were sampled in the Lizard Island area (lat. 14° 40' S, long. 154° 28' E) from March 1990 to February 1992. Fishes were caught by recreational and commercial fishermen using hook and line (n=184) and by recreational spearfishermen (n=94). Individuals smaller than 20–cm total length are usually not vulnerable to line fishing, so they were caught around Lizard Island by scuba divers using fence nets (n=32). Fork length (FL, cm), standard length (SL, cm) and total weight (TW, g) were measured for each fish. FL is defined as the length from the front of the snout to the caudal fork, and SL is defined as the length from the front of the upper lip to the posterior end of the vertebral column. A simple linear regression of the form FL= a + b*SL was used to describe the relationship between FL and SL. To describe the relationship between FL and TW the variables were logarithmically transformed and the linearized version of the power function $TW(g) = a*FL(\mathrm{cm})b$ was fitted to the data.

In the coral trout, the sagittae are the largest of the three pairs of otoliths and were used for readings. Sagittae were removed, cleaned, weighed, and stored dry. Left and right sagittae, when intact, were weighed to the nearest milligram. Otoliths were prepared and read as described by Ferreira and Russ (1992). To increase contrast between bands, whole otoliths were burned lightly on a hot plate at 180°C (Christensen, 1964). Both right and left sagitta were read whole under reflected light with a dissecting microscope at 16× magnification. The otoliths, with the concave side up, were placed in a black container filled with immersion oil. Subsequently, the left sagittae was prepared for reading by embedding in epoxy resin (Spurr, 1969) and sectioning transversely through the core with a Buehler Isomet low-speed saw. Sections were mounted on glass slides with Crystal Bond 509 adhesive, ground on 600– and 1200–grade sand paper, polished with 0.3–μ alumina micropolish and then examined under a dissecting microscope at 40× magnification with reflected light and a black background (Fig. 1). Annuli were counted from the nucleus to the proximal surface of the sagitta along the ventral margin of the sulcus acousticus.

Terminology for otolith readings followed definitions of Wilson et al. (1987). Two experienced readers independently counted opaque zones (annuli) in each whole and sectioned otolith of a random subsample (n=136) to assess the precision and accuracy of countings obtained by the two methods. The precision of age estimates was calculated with the Index of Average Percent Error (IAPE), (Beamish and Fournier, 1981). Results obtained from whole and sectioned otoliths were compared by plotting the difference between readings obtained from whole and sectioned otoliths (Section Age-Whole age) against Section Age. The results of this comparison indicated that whole otolith readings tended to be lower than readings from sectioned otoliths when more than six rings occurred in the otolith. Therefore, remaining otoliths were read whole first and, if the number of rings was higher than six or the whole otolith was considered unreadable, the otolith was sectioned and counts were repeated. The results were accepted and used in the analysis when the counts of the two readers agreed. If the counts differed, the readings were repeated once and if the counts still differed, the fish was excluded from the analysis.

Ages were assigned based on annulus counts and knowledge of spawning season. The periodicity of annulus formation was determined with the use of tetracycline labelling. From August 1990 to February 1992, 80 fishes were caught in a trapping program at Lizard Island fringing reef (Davis, 1992[2]),

[2] C. Davies. 1992. James Cook University, Townsville, Q4811, Australia, unpubl. data.

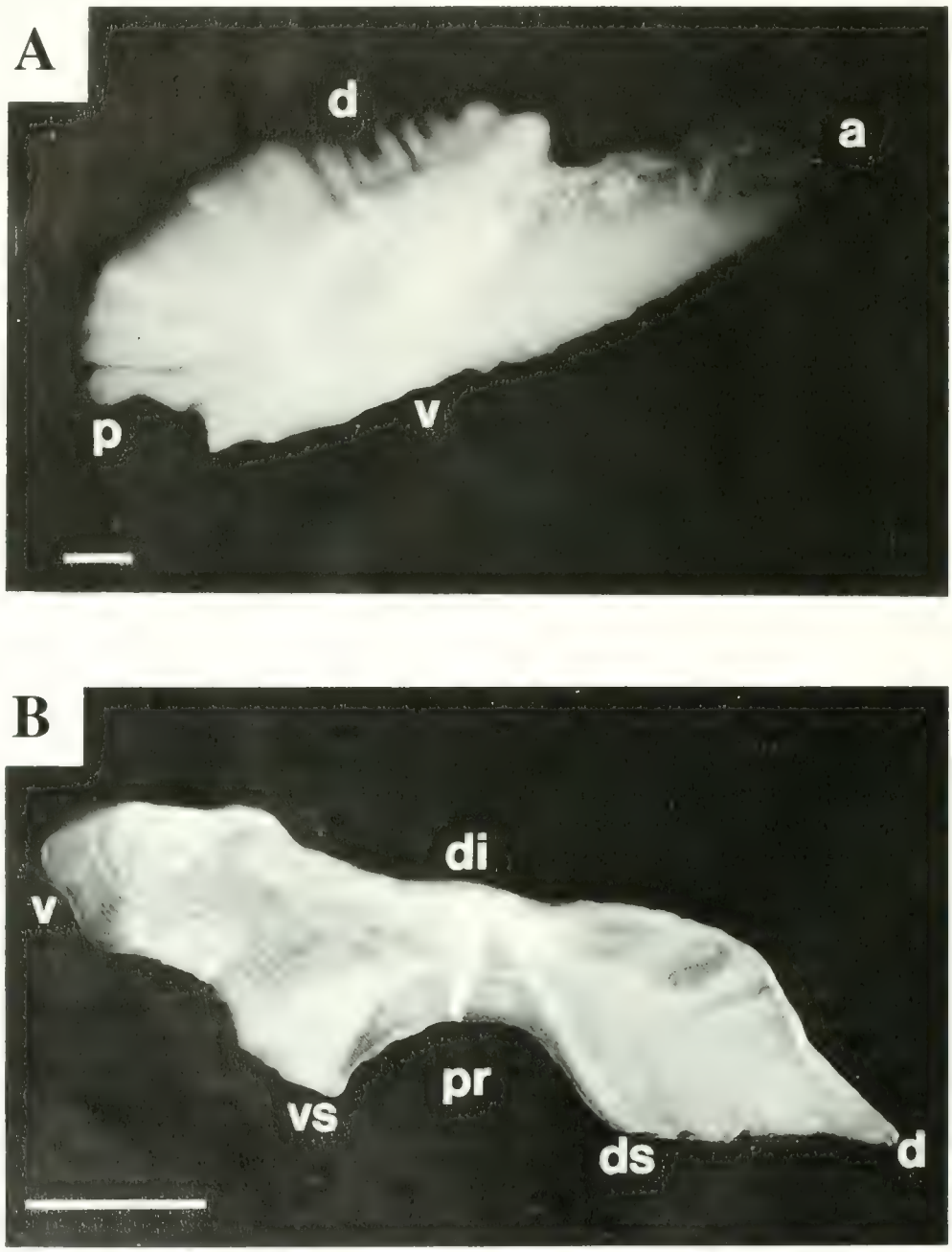

Figure 1

Whole (**A**) and sectioned (**B**) otolith of an 11–year-old coral trout, *P. leopardus*, under reflected light with a black background showing alternating pattern of translucent and opaque bands; **a** = anterior, **p** = posterior, **d** = dorsal, **v** = ventral, **di** = distal, **pr** = proximal, **ds** = dorsal sulcus, **vs** = ventral sulcus. Scale bar = 1 mm

tagged with T-bar anchor tags and injected with tetracycline hydrochloride before being released. The fish were injected in the coelomic cavity under the pelvic fin with a dosage of 50 mg of tetracycline per kg of fish (McFarlane and Beamish, 1987), in a concentration of 50 mg per mL of sterile saline solution. Five fish were recaptured after periods of at least one year at large. Two of those fish were reinjected at the time of recapture and kept in captivity for periods of three to four months.

To determine the time of formation of the first annulus, five young of the year were captured with

fence nets. Three of these fishes were injected with tetracycline at the time of capture, and all five fish were kept in captivity for periods of 3 to 17 months. The otoliths of the fishes treated with tetracycline were removed, sectioned, and observed under fluorescent light. To determine time of formation of the translucent and opaque zones, the distances between events for which time of occurrence was known (i.e., between two tetracycline bands or between a tetracycline band and the margin of the otolith) were measured on otolith sections and plotted against the corresponding time interval. The relative positions of the translucent and opaque zones to these marks were then measured and plotted on the same scale. While this method does not provide real distances, it standardizes the measurements allowing for comparison between fish of different ages.

The relation between otolith weight, fish size (length and weight), and age was analyzed. Otolith weight was plotted against FL for each age class separately. A multiple linear regression model was fitted in a step-wise manner to predict age from otolith weight and fish size and to predict otolith weight from age and fish size. The inclusion level for the independent variables was set at P=0.10. The assumptions of normality and homoscedasticity were tested by plotting the residuals from the regression models.

The growth models were fitted to the data and their coefficients and standard errors estimated by means of standard non-linear optimization methods (Wilkinson, 1989). As the plot of the length-at-age data indicated, some form of asymptotic growth, Schnute's (1981) reformulation of the von Bertalanffy growth equation for length in which a≠0 was fitted to the data:

$$L_t = y1^b + (y2^b - y1^b)\left\{\frac{1-e^{-a(t-t1)}}{1-e^{-a(t2-t1)}}\right\}^{\frac{1}{b}}$$

where L_t is length at age; $t1$ and $t2$ are ages fixed as 1 and 14 respectively ; $y1$ and $y2$ are estimated sizes at these ages; and a and b are the parameters which indicate if the appropriate growth curve lies closer to a three or two parameter sub-model. By limiting parameter values, the data were used directly in selecting the appropriate sub-model, namely the generalized von Bertalanffy, Richards, Gompertz, Logistic, or Linear growth models. Subsequently, the original von Bertalanffy (1938) growth equation for length $L_t = L_\infty (1 - e^{-K(t-to)})$was fitted to the data. L^t is length at age; L_∞ is the asymptotic length, K is the growth coefficient, t is age, and t_o is the hypothetical age at which length is zero.

To evaluate the effects of gear selectivity (and consequently varying size and age composition) on the estimates of growth parameters, the von Bertalanffy growth equation was fitted first to data collected by line and spear fishing only and then to the same data combined with the fence-net sample composed of younger fish.

Results

Otolith reading

In the coral trout, the sagittae presented a pattern of alternating translucent zones and wide opaque zones (annuli) with no sharp contrast between zones (Fig. 1). The first two annuli were notably wider and less well defined than the subsequent ones in sectioned otoliths. Whole sagittae were used to confirm the presence of these first annuli.

In whole otoliths, annuli were clearly distinguishable and easy to count along the dorsal side of the otolith, where up to 12 rings were counted in some otoliths. However, readings from whole otoliths tended to be lower than readings from sectioned otoliths when more than six rings were present, and this tendency increased with the mean number of rings, particularly after ten rings. (Fig. 2). Tetracycline-labelled otoliths validated the periodicity of annuli in sectioned otoliths, indicating that whole otolith readings tend to underestimate age of >10–year-old fishes. A comparison between results of

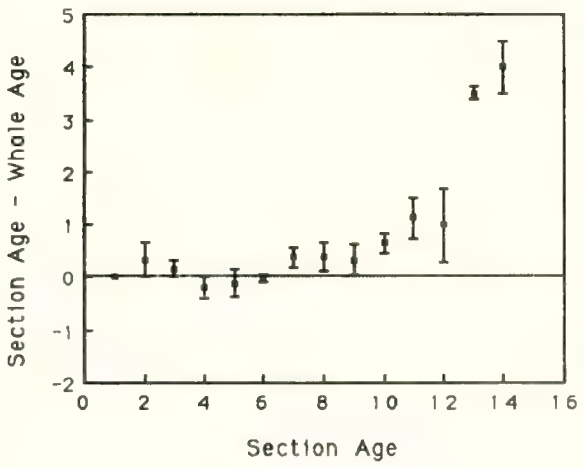

Figure 2

Average difference between counts obtained from sectioned and whole otoliths (Section Age-Whole Age) of coral trout, *P. Leopardus*, plotted against Section Age. Error bars show standard error.

countings performed on whole and sectioned otoliths showed that, in the sub-sample analysed, the Index Average Percent Error (IAPE) of Beamish and Fournier (1981), was lower for counts performed on whole (6.7%) than for counts performed on sectioned otoliths (12.1%). For the total sample, where readings from whole and sectioned otoliths were integrated, the IAPE was reduced to 5.1%.

Otolith growth

Otolith weight was directly related to age and an exponential function of fish length (Fig. 3). Within each age class, otolith weight was positively correlated with fork length for most classes (Table 1), indicating a tendency for larger fish to have larger otoliths than smaller fish of the same age. The weight of the otolith was a good predictor of age and accounted alone for 89% of the variability in age of the coral trout (r^2=0.889, P<0.0001), with fork length accounting for 1.5% (partial r^2= 0.015). Otolith weight was a function of age and fish size, as indicated by the results of the multiple regression fitting. The interaction between age and fork length alone accounted for 89% of the variability (r^2=0.892, P<0.0001)

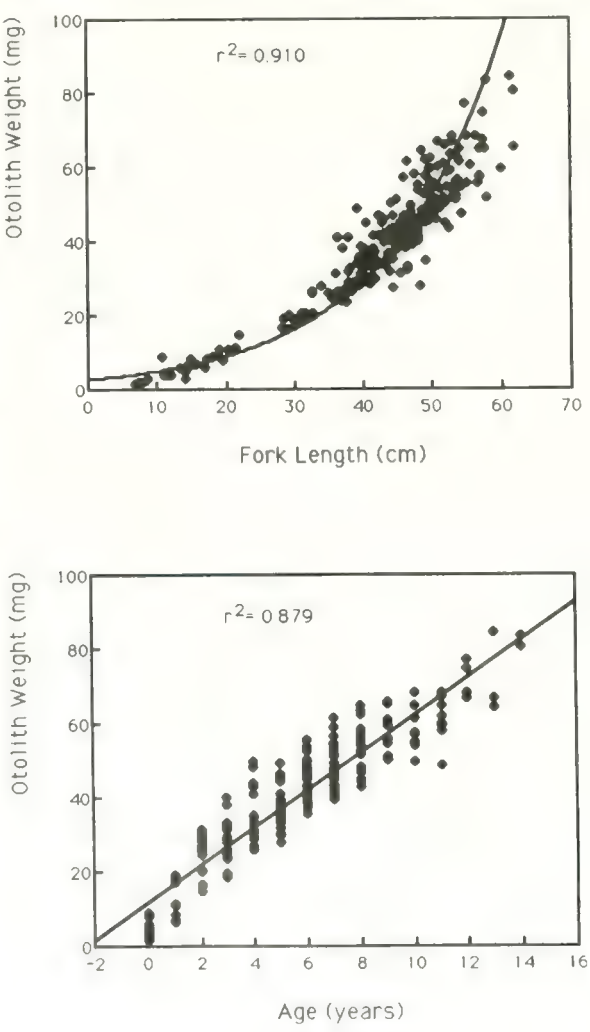

Figure 3

Relation between otolith weight and Fork Length (FL) and otolith weight and age for coral trout, *P. leopardus*.

Validation of annulus formation

All fishes treated with tetracycline displayed clear fluorescent marks in their otoliths (Fig. 4). The results obtained for recaptured and captive fish, ranging in age from one to eight years, showed that annuli are formed once per year (Fig. 5). The first annulus is formed in the otoliths of the juvenile coral trout during their first year of life (Fig. 6). The relative positions of the fluorescent bands, in relation to the otolith margin and the translucent and opaque zones (annuli), indicated that the formation of the annulus occurred mainly during winter and early spring (Figs. 5 and 6).

Growth model

The samples obtained from line-fishing and spearfishing were selective towards individuals larger than 25 cm FL. Consequently, the 0+ age class was not represented in this sample and the age-1 year class was represented by only four individuals (Fig. 7). The sample collected with fence nets, composed of individuals from the smaller size classes, consisted totally of individuals of the 0+ and 1+ year classes (Fig. 7). Table 2 shows the results obtained when fitting the growth model to the data including all age classes and to the data including only age ≥2+.

Table 1

Correlation between otolith weight (mg) and fork length (cm) for each age class of the coral trout *P. leopardus*.

Age	r^2	P<	df	Age	r^2	P<	df
0	0.826	0.0001	18	8	0.481	0.0001	19
1	0.972	0.0001	10	9	0.405	0.0001	12
2	0.829	0.0001	27	10	0.120	no sig.	8
3	0.747	0.0001	19	11	0.937	0.0001	7
4	0.652	0.0001	18	12	0.526	no sig.	3
5	0.650	0.0001	30	13	0.993	0.05	2
6	0.489	0.0001	43	14	0.049	no sig.	2
7	0.514	0.0001	30				

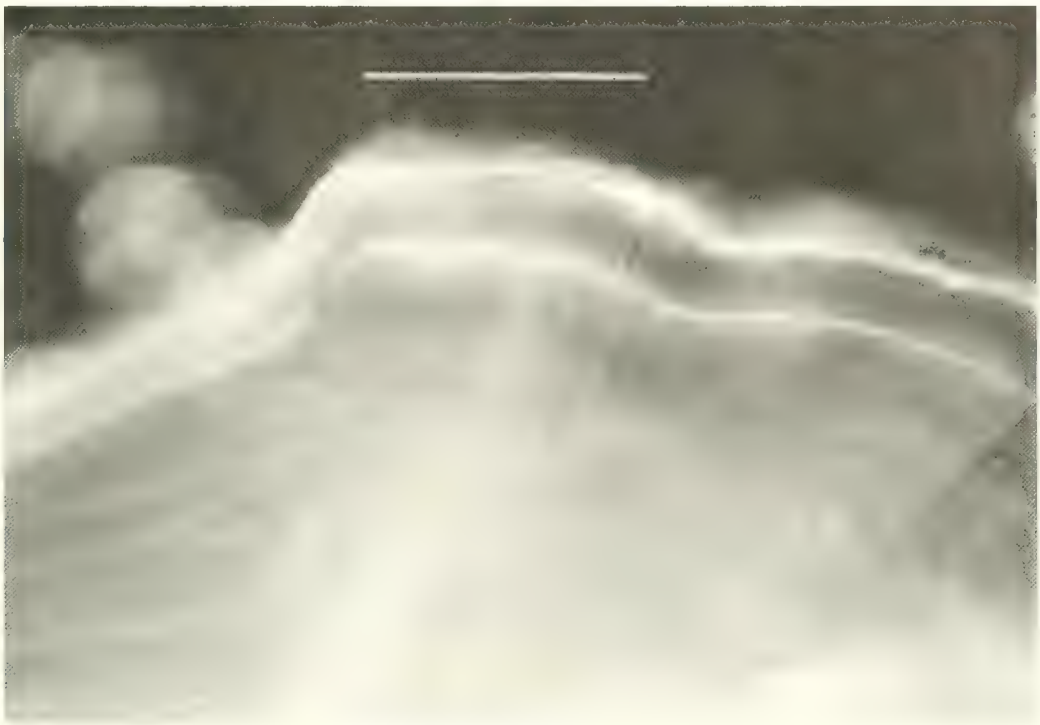

Figure 4

Sectioned otolith of a recaptured individual coral trout, *P. leopardus* (n° 0057), showing fluorescent band. Scale Bar = 0.25 mm

When fitting Schnute's model to both sets of data, the value of the parameter b was very close to 1. In the boundary where $b = 1$, the curve was reduced to a three parameter model that corresponds to the von Bertalanffy curve for length (Schnute, 1981). The resulting growth model for all age classes, in the form of a von Bertalanffy model, was

$$L_t = 52.2\left(1 - e - 0.354\,(t + 0.766)\right)\ r^2 = 0.895 \text{ (Fig. 8).}$$

Table 2

Von Bertalanffy growth parameters V.B. and respective standard errors (SE), correlation coefficients (r^2) and degrees of freedom (df) for the growth curve fitted to all data and to the data for coral trout, *P. Leopardus*, ≥2 year old only.

	L_∞ (SE)	K (SE)	t_o (SE)	r^2	df
V.B. all ages	52.20 (0.768)	0.354 (0.024)	−0.766 (0.097)	0.895	310
V.B. age ≥2+	61.29 (3.483)	0.132 (0.030)	−4.660 (1.024)	0 622	272

The results obtained when fitting the growth curve to all data and to the data for fish ≥2+ years old only were quite different (Table 2). From age-2 onwards, the growth rate is much slower than the one estimated by using all age classes, as indicated by the growth coefficient K. Consequently, the estimated L_∞ is larger and the estimated t_o is a very large, negative value. The resulting growth model was

$$L_t = 61.29\left(1 - e - 0.132\,(t + 4.66)\right)\ r^2 = 0.622 \text{ (Fig. 9).}$$

No systematic trend in the residuals was observed (normality test $P>0.1$) (Figs. 8 and 9).

The relation between fork length (FL) and the standard length (SL) was

$$SL = -0.308 + 0.852 * FL,\ r^2 = 0.994,$$

and the relationship between FL and Total Weight (TW) was

$$TW = 0.0079 * FL^{3.157},\ r^2 = 0.967.$$

Discussion

While some comparisons between readings of whole and sectioned otoliths have indicated good agree-

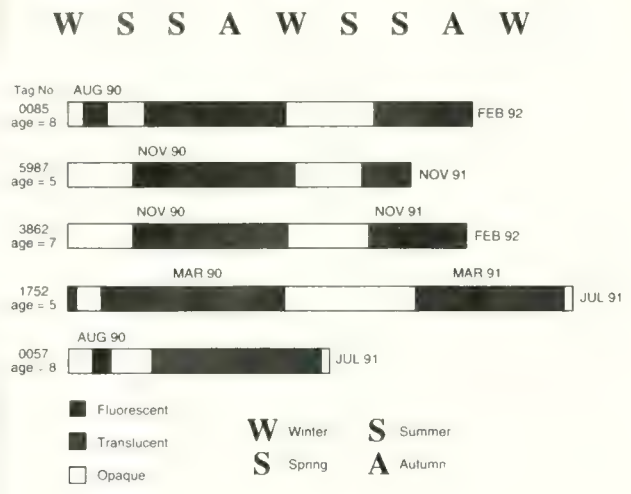

Figure 5

Diagrammatic representation of otoliths of mark-released-recaptured coral trout, *P. leopardus*, treated with tetracycline showing relative positions of the fluorescent bands, otolith margin, translucent and opaque zones. Bars represent only the distal part of the radius of the otolith section, measured from the nucleus to the proximal surface of the sagitta along the ventral margin of the sulcus acousticus. The dates on the top of the bars indicate time of tetracycline treatment and the dates on the end of the bars indicate time of recapture.

ment (Boehlert, 1985; Maceina and Betsill, 1987), others have suggested that reading whole otoliths underestimates true age and that this problem becomes worse with fish age (Boehlert, 1985; Hoyer et al., 1985). This is mainly due to the fact that in many species, sagittae growth is asymmetrical (Irie, 1960). Growth appears to be linear only up to a certain age or size, after which additions occur mainly on the interior proximal surface, along the sulcus region (Boehlert, 1985; Brothers, 1987; Beamish and McFarlane, 1987). That seems to be the case for the coral trout, as comparison of results of whole and sectioned otoliths indicated that lateral views did not reveal many of the annual growth zones in older individuals. However, whole otoliths require much less time for analysis than sectioned ones and seem to provide more precise readings. Therefore, it is useful to know the limit of reliability of whole readings and to define the conditions appropriate for its use.

Like the inshore coral trout *Plectropomus maculatus* (Ferreira and Russ, 1992), the common coral trout *P. leopardus* is a relatively long-lived, slow-growing species. The results on growth and longevity obtained here differ somewhat from those of previous studies. Goeden (1978), using the Petersen method, identified age cohorts up to age 5+ for *P. leopardus*. However, the limitations of the use of length-frequency data to estimate age of long-lived fish are well known (Manooch, 1987; Ferreira and Vooren, 1991). Mcpherson et al. (1988), using counts of annuli in whole otoliths, were able to age fish up to seven years old. Longevity was probably underestimated in their study as counts were performed only on whole otoliths. More recently, Brown et al. (1992)[3] analyzed whole and sectioned otoliths of coral trout from the same area as Mcpherson et al. (1988) and were able to count up to 14 rings. Loubens (1980) counted annuli from burnt and broken otoliths and estimated a maximum longevity for

[3] Brown, I. W., L. C. Squire, and L. Mikula. 1992. Effect of zoning changes on the fish populations of unexploited reefs. Stage 1: pre-opening assessment. Draft interim report to the Great Barrier Reef Marine Park Authority, Townsville, Australia, 27 p.

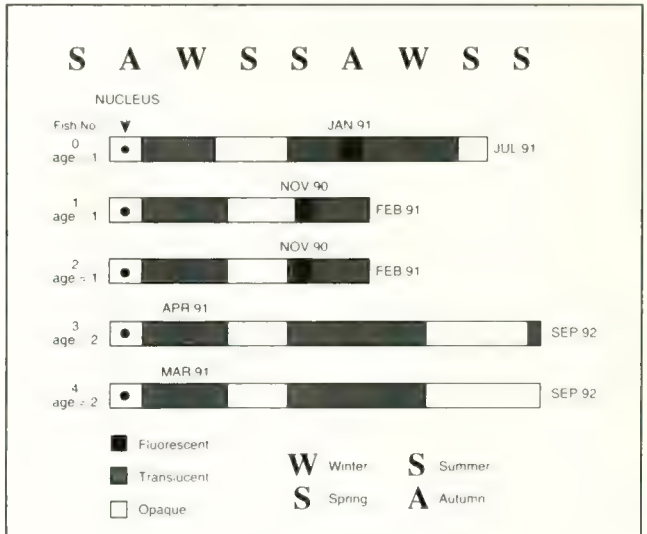

Figure 6

Diagrammatic representation of otoliths of young-of-the year coral trout, *P. leopardus*, kept in captivity, showing relative positions of the fluorescent bands, otolith margin, translucent, and opaque zones. Bars represent the whole radius of the otolith section, measured from the nucleus to the proximal surface of the sagitta along the ventral margin of the sulcus acousticus. The dates on the top of the bars indicate time of tetracycline treatment or capture and the dates on the end of the bars indicate time of death.

P. leopardus of 19 years in New Caledonia. These higher estimates of longevity suggest that coral trout at Lizard Island could also attain older ages. In this case, the absence of fishes older than 14 years of age in the sample collected at Lizard Island could be related to local levels of fishing pressure.

In the present work, the results of tetracycline labelling indicated that in the otoliths of *P. leopardus* the opaque zone (annulus) was formed during the winter and spring months whereas the translucent zone was formed during summer and autumn. Though the physiological basis for the formation of optically distinct zones in calcified structures has not been directly established, their presence has been commonly associated with varying growth rates, influenced by temperature, photoperiod, feeding rate, or reproductive cycle (see Casselman, 1983, and Longhurst and Pauly, 1987, for review). On a daily basis, it has been demonstrated that the translucent zone, or accretion zone, is formed during the phase of more active otolith growth, and the opaque or discontinuous zone is formed during growth stagnation (Mugiya et al., 1981; Watabe et al., 1982). Mosegaard et al. (1988) examined the effect of temperature, fish size, and somatic growth rate on otolith growth rate and suggested that metabolic activity, not necessarily somatic growth rate, governs otolith growth. Thus, if the formation of the opaque zone in the coral trout otoliths is associated with a period of reduced metabolic activity, an external determining factor could be temperature, as the lowest values for water temperature around Lizard Island are observed during winter and early spring.[4] Annulus formation occurred in otoliths of juveniles and adults of coral trout during the same period, suggesting that reproduction is not a determining factor.

The growth of the otolith was continuous with age but apparently related to somatic growth. A similar pattern has been observed for other species of fish (Beckman et al., 1991). Otolith weight was the best predictor of age in the linear model, explaining as much variation in age as fork length in the von Bertalanffy model.

The main criteria for choosing a growth curve are quality of fit and convenience, differing according to whether the need is for a mathematical description of a detailed physiological growth process or for fishery management (Moreau, 1987). The results obtained here indicated clearly that the von Bertalanffy model adequately described the growth of the coral trout. Schnute's model was useful because of its flexibility and the stability of its parameters.

Figure 7

Age-at-length data for coral trout, *P. leopardus*, from Lizard Island captured by each sampling gear used in this study.

As most fishing gears are selective towards a certain size (Ricker, 1969), and smaller sizes are not usually available, it is common that growth curves are fitted to truncated data representing only part of the population. For the coral trout, because of gear selectivity and legal size restrictions (legal minimum=35 cm TL), only fish of 2+ years were captured by line- and spear-fishing. However, the first three years of life represent the period of fastest growth, after which the growth pattern changes considerably. As a result, much slower growth rates were obtained when the growth curve was fitted only to the age classes recruited to the fishery. The effects of different age ranges on estimated von Bertalanffy growth parameters have been recognized for many years (Knight, 1968; Hirschhorn, 1974) and greatly compromise comparisons of growth rates between populations (Mulligan and Leaman, 1992).

Furthermore, one effect of size-dependent mortality is the selective removal of fast-growing individuals (Ricker, 1969; Miranda et al., 1987). Thus, it is likely that the average size of the youngest age groups recruited to the fishery will be biased towards the largest, fast-growing individuals. This

[4] Lizard Island Research Station. 1992. LIRS, PMB 37, Cairns, Queensland 4870, Australia. Unpubl. data.

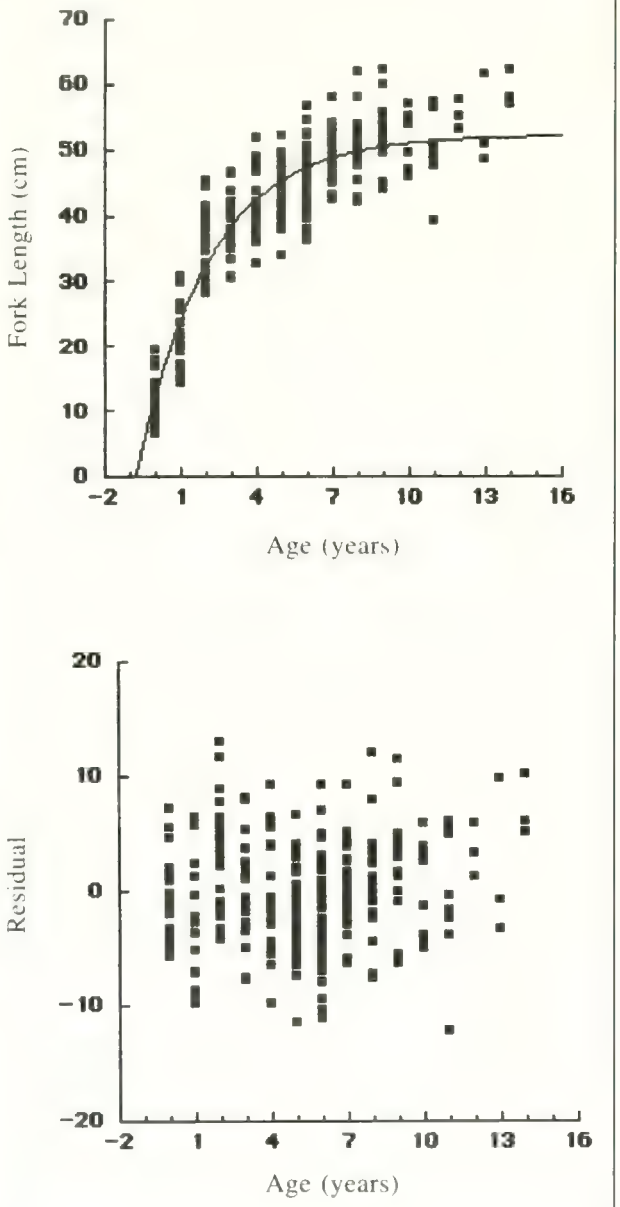

Figure 8

Von Bertalanffy growth curve fitted to length-at-age data of all age classes of coral trout, *P. leopardus*, and plot of residuals.

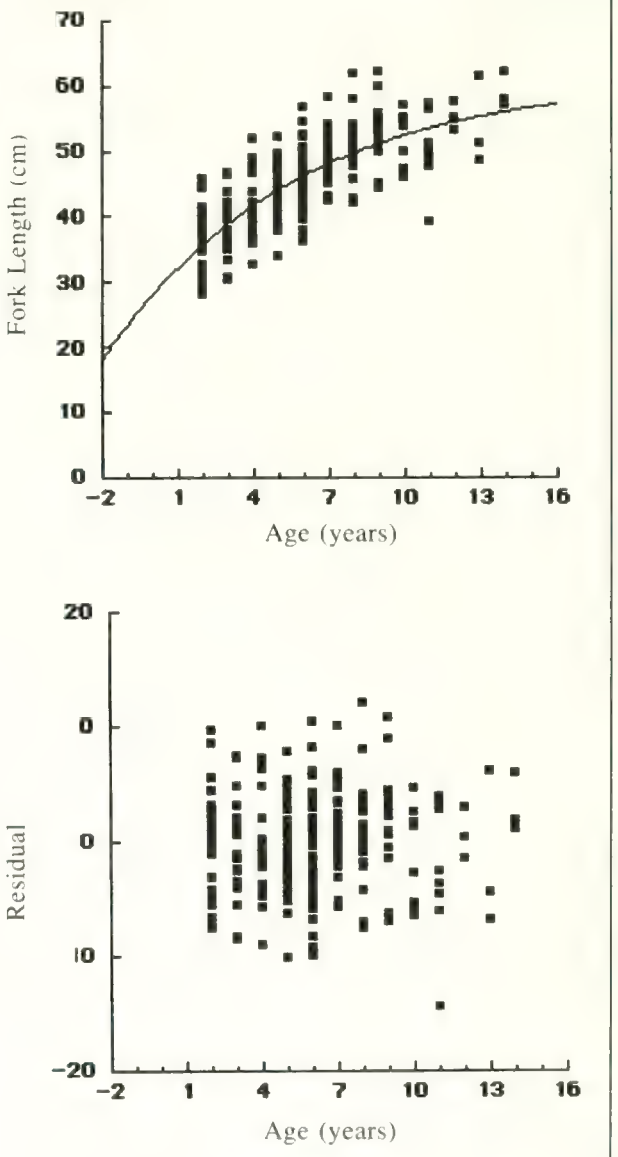

Figure 9

Von Bertalanffy growth curve fitted to length-at-age data of ≥2+ years old coral trout, *P. leopardus*, and plot of residuals.

seems to be the case for age class 2+, the length of which is underestimated by the model including all data (Fig. 8). Exclusion of younger ages under these circumstances would further enhance the underestimation of K, as well as overestimation of L_∞ (Mulligan and Leaman, 1992).

Recent research has suggested the possibility of different growth processes within a population with associated selective fishing mortality (Parma and Deriso, 1990) and natural mortality (Mulligan and Leaman, 1992). The large variability in size at a given age observed for the coral trout suggests the occurrence of individual variability in growth. The reliability of methods of growth estimation like length-frequency analysis and growth increments from marking-recapture techniques, is greatly affected by this kind of variation (Sainsbury, 1980), further enhancing the importance of obtaining validated length-at-age estimates for exploited fish populations. The results of selective mortality are a direct effect of growth variability on the dynamics of abundance, and failure to consider the effects

of different growth potentials can result in gross overestimation of optimal fishing levels (Parma and Deriso, 1990).

The absence of marked seasonal changes in low latitudes has led to the general belief that tropical fishes do not form annual rings in their calcified structures (Pannella, 1974). Consequently, most of the studies of age determination of tropical fishes have concentrated on examination of daily rings. This technique, however, is time consuming and limited to younger ages (see Longhurst and Pauly, 1987, and Beamish and McFarlane, 1987, for review). The presence of annual marks in otoliths has been validated for an increasing number of species of tropical fishes (Samuel et al., 1987; Fowler, 1990; Ferreira and Russ, 1992; Lou, 1992) showing the potential of this technique to be used routinely in tropical fishery management.

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Literature cited

Beamish, R. J., and D. A. Fournier.
1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982–983.

Beamish, R. J., and G. A. McFarlane.
1987. Current trends in age determination methodology. *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 15–42. Iowa State Univ. Press, Ames.

Beckman, D. W., A. L. Stanley, J. H. Render, and C. A Wilson.
1991. Age and growth-rate estimation of sheepshead *Archosargus probatocephalus* in Louisiana waters using otoliths. Fish. Bull. 89 (1):1–8.

Beverton, R. J. H., and S. J. Holt.
1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food (G.B.), Ser. 2 (19), 533 p.

Boehlert, G. W.
1985. Using objective criteria and multiple regression models for age determination in fishes. Fish. Bull. 83 (2):103–117.

Brothers, E. B.
1987. Methodological approaches to the examination of otoliths in aging studies. *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 319–330. Iowa State Univ. Press, Ames.

Casselman, J. M.
1983. Age and growth assessment of fish from their calcified structures: techniques and tools. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8, p. 1–17.
1990. Growth and relative size of calcified structures of fish. Trans. Am. Fish. Soc. 119:673–688.

Chen, Y., D. A. Jackson, and H. H. Harvey.
1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. Can. J. Fish. Aquat. Sci. 49:1228–1235.

Christensen, J. M.
1964. Burning of otoliths, a technique for age determination of soles and other fish. J. Cons. perm. int. Explor. Mer. 29:73–81.

Ferreira, B. P., and C. M. Vooren.
1991. Age, growth and structure of vertebra in the school shark *Galeorhinus galeus* (Linnaeus, 1758) from Southern Brazil. Fish. Bull. 89 (1):19–31.

Ferreira, B. P., and G. R. Russ.
1992. Age, growth and mortality of the inshore coral trout *Plectropomus maculatus* (Pisces: Serranidae) from the Central Great Barrier Reef, Australia. Aust. J. Mar. Freshwater Res. 43:1301–1312.

Fowler, A. J.
1990. Validation of annual growth increments in the otoliths of a small, tropical coral reef fish. Mar. Ecol. Prog. Ser. 64:25–38.

Gallucci, V. F., and T. J. Quinn.
1979. Reparameterizing, fitting and testing a simple growth model. Trans. Am. Fish. Soc. 108:14–25.

Goeden, G. B.
1978. A monograph of the coral trout *Plectropomus leopardus* (Lacepede). Qld. Fish. Serv., Res. Bull. (1):1–42.

Hirschhorn, G.
1974. The effect of different age ranges on estimated Bertalanffy growth parameters in three fishes and one mollusk of the northeastern Pacific Ocean. *In* T. B. Bagenal (ed.), Ageing of fish, p. 13–27. Unwin Bros., Surrey, England.

Hoyer, M. V., J. V. Shireman, and M. J. Maceina.
1985. Use of otoliths to determine age and growth of largemouth bass in Florida. Trans. Am. Fis. Soc. 114:307–309.

Irie, T.
1960. The growth of the fish otolith. J. Fac. Fish. Anim. Husb. Hiroshima Univ. 3 (1):203–229.

Kimura, D. K.
1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77:756–776.

Knight, W.
1968. Asymptotic growth: an example of nonsense disguised as mathematics. J. Fish. Res. Board. Can. 25 (6):1303–1307.

Longhurst, A. R., and D. Pauly.
1987. Ecology of tropical oceans. Acad. Press, San Diego, 407 p.

Lou, D. C.
1992. Validation of annual growth bands in the otolith of tropical parrotfishes (*Scarus schlegeli* Bleeker). J. Fish. Biol. 41:775–790.

Loubens, G.
1980. Biologie de quelques especes de poissons du lagon Neo-Caledonien. III: Croissance. Cahiers de l'Indo-pacifique 2:101–153.

Maceina, M. J., and R. K. Betsill.
1987. Verification and use of whole otoliths to age white crappie. *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 267–278. Iowa State Univ. Press, Ames.

Manooch III, C. S.
1987. Age and growth of snappers and groupers. *In* J. J. Polovina and S. Ralston (eds.), Tropical snappers and groupers. Biology and Fisheries Management, p. 329–374. Westview Press, Inc., Boulder.

McFarlane, G. A., and R. J. Beamish.
1987. Selection of dosages of oxytetracycline for age validation studies. Can. J. Fish. Aquat. Sci. 44:905–909.

Mcpherson, G., L., Squire and J. O'Brien.
1988. Demersal reef fish project 1984–85: age and growth of four important reef fish species. Fisheries Research Branch Technical Report No. FRB 88/6. Queensland Department of Primary Industries, Australia, 38 p.

Miranda, L. E., W. M. Wingo, R. J. Muncy, and T. D. Bates.
1987. Bias in growth estimates derived from fish collected by anglers. *In* R. C. Summerfelt and G. E. Hall (eds.) Age and growth of fish, p. 211–220. Iowa State Univ. Press, Ames.

Moreau, J.
1987. Mathematical and biological expressions of growth in fishes: recent trends and further developments *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 81–114. Iowa State Univ. Press, Ames.

Mosegaard, H., H. Svedang, and K. Taberman.
1988. Uncoupling of somatic growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. 45:1514–1524.

Mugiya, Y., N. Watabe, J. Yamada, J. M. Dean, D. G. Dunkelberger, and M. Shimizu.
1981. Diurnal rhythm in otolith formation in the goldfish, *Carassius auratus*. Comp. Biochem. Physiol. 68A:659–662.

Mulligan, T. J., and B. M. Leaman.
1992. Length-at-age analysis: can you get what you see? Can. J. Fish. Aquat. Sci. 49:632–643.

Pannella, G.
1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. *In* T. B. Bagenal (ed.), Ageing of fish, p. 28–36. Unwin Bros., Surrey, England.

Parma, A., and R. B. Deriso.
1990. Dynamics of age and size composition in a population subject to size-selective mortality: effects of phenotypic variability in growth. Can. J. Fish. Aquat. Sci. 47:274–289.

Ralston, S.
1987. Mortality rates of snappers and groupers. *In* J. J. Polovina and S. Ralston (eds.), Tropical snappers and groupers. Biology and Fisheries Management, p. 375–404. Westview Press, Inc., Boulders.

Randall, J. E.
1987. A preliminary synopsis of the groupers (Perciformes: Serranidae: Epinephelinae) of the Indo-Pacific region. *In* J. J. Polovina and S. Ralston (eds.), Tropical snappers and groupers. Biology and Fisheries Management, p. 89–187. Westview Press, Inc., Boulders.

Randall, J. E., and D. F. Hoese.
1986. Revision of the groupers of the Indo-Pacific genus *Plectropomus* (Perciformes: Serranidae) (13). Bernice Pauahi Bishop Museum, Honolulu, Hawaii, 31 p.

Ricker, W. E.
1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. J. Fish. Res. Board Can. 26:479–541.

Sainsbury, K. J.
1980. Effect of individual variability on the von Bertalanffy growth equation. Can. J. Fish. Aquat. Sci. 37:241–247.

Samuel, M., C. P. Mathews, and A. S. Baazeer.
1987. Age and validation of age from otoliths for warm water fishes from the Arabian Gulf. *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 253–266. Iowa State Univ. Press, Ames.

Schnute, J.
1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38:1128–1140.

Spurr, A. R.
1969. A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. (26):31–34.

Trainor, N.
1991. Commercial line fishing. *The Queensland Fisherman*, March:17–25.

von Bertalanffy, L.
1938. A quantitative theory of organic growth. II: Inquires on growth laws. Hum. Biol. 10:181–213.

Watabe, N., K. Tanaka, J. Yamada, and J. Dean.
1982. Scanning electron microscope observations of the organic matrix in the otoliths of the teleost fish *Fundulus heteroclitus* (L.)and *Tilapia nilotica* (L.). J. Exp. Mar. Biol. Ecol. 58:127–134.

Wilkinson, L.
1989. SYSTAT: the system for statistics. Evanston, IL: SYSTAT, Inc.

Wilson, C. A., R. J. Beamish, E. B. Brothers, K. D. Carlander, J. M. Casselman, J. M. Dean, A. Jearld, E. D. Prince, and A. Wild.
1987. Glossary. *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 527–530. Iowa State Univ. Press, Ames,

Abstract.— Red drum, *Sciaenops ocellatus*, from Mosquito Lagoon, east-central Florida, were examined for variation in products of nine polymorphic nuclear-gene (allozyme) loci and in mitochondrial (mt)DNA restriction sites. Genetic data from Mosquito Lagoon fish were compared to similar data from red drum sampled from the northeastern Gulf of Mexico (Gulf) and the Carolina coast of the southeastern United States. Significant heterogeneity among red drum from the three areas was found in the frequencies of inferred alleles at two to three allozyme loci and in the frequencies of six mtDNA haplotypes. Red drum from Mosquito Lagoon were as differentiated genetically from red drum in the northeastern Gulf and Carolina coast as the latter two were from each other. Genetic data are consistent with the hypothesis that red drum in Mosquito Lagoon are self-contained and at least partially isolated from red drum in other U.S. waters.

Genetic distinctness of red drum (*Sciaenops ocellatus*) from Mosquito Lagoon, east-central Florida*

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Over the past five years, our laboratory has carried out studies of spatial and temporal genetic variation among red drum (*Sciaenops ocellatus*) from the northern Gulf of Mexico (Gulf) and the Carolina coast of the southeastern United States (Bohlmeyer and Gold, 1991; Gold and Richardson, 1991; Gold et al., 1993, in press). Red drum currently support important recreational fisheries in both the northern Gulf and U.S. Atlantic (Matlock, 1984; Mercer, 1984), and both fisheries are now regulated to reduce growth and recruitment overfishing (Swingle et al., 1984[1]; Goodyear, 1989[2]). Collectively, our genetic data have indicated that red drum in U.S. waters are subdivided with weakly differentiated subpopulations in the northern Gulf and along the Carolina coast. No genetic heterogeneity has been found among red drum from different localities within either the northern Gulf or Carolina coast (Gold et al., 1993, in press). The genetic data are consistent with several aspects of red drum biology and life history that suggest red drum dispersal and gene flow among contiguous bays and estuaries could be extensive. These include 1) transport of eggs, larvae, or juveniles from spawning localities near the mouths of bays or estuaries to adjacent bays or estuaries by oceanic currents (Lyczkoski-Schultz et al., 1988[3]), 2) movement of sexually-mature adults from bay or estuarine juvenile nurseries into deeper, offshore waters prior to spawning (Matlock, 1984), and 3) formation of large, offshore schools that can migrate extensively (Overstreet, 1983; Matlock, 1984; Swingle et al., 1984[1]).

In this study, data on allozyme and mitochondrial (mt)DNA variation among red drum sampled from Mosquito Lagoon on the east coast of Florida are presented and compared to data from previous studies. The goal of the study was to

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[1] Swingle, W., T. Leary, D. Davis, V. Blomo, W. Tatum, M. Murphy, R. Taylor, G. Adkins, T. McIlwain, and G. Matlock. 1984. Fishery profile of red drum. Gulf of Mexico Fish. Mngmt. Council and Gulf States Mar. Fish. Comm., Lincoln Cntr., Suite 331, 5401 West Kennedy Blvd., Tampa, FL.

[2] Goodyear, C. P. 1989. Status of red drum stocks of the Gulf of Mexico: report for 1989. Contrib. CRD 88/89–14, Southeast Fish. Cntr., Miami Lab., Coast. Res. Div., 75 Virginia Beach Drive, Miami, FL.

[3] Lyczkowski-Schultz, J., J. P. Steen Jr., and B. H. Comyns. 1988. Early life history of red drum (*Sciaenops ocellatus*) in the northcentral Gulf of Mexico. Mississippi-Alabama Sea Grant Consortium (Project No. R/LR-12). Gulf Coast Res. Lab., P.O. Box 7000, Ocean Springs, unpubl. ms.

test the hypothesis that red drum from Mosquito Lagoon and other U.S. waters are genetically homogeneous. Red drum in Mosquito Lagoon are of particular interest because they may represent a self-contained, at least partially isolated subpopulation. Evidence for the latter includes documentation within the system of both post-spawning females and red drum eggs (Murphy and Taylor, 1990; Johnson and Funicelli, 1991). In addition, physical access to the Atlantic from the lagoon is limited. In brief, Mosquito Lagoon (Fig. 1) is long and narrow (54 km × 4 km) and is separated from the Atlantic by a barrier beach. The lagoon represents the northern part of the Indian River lagoonal system and has two narrow outlets: one, Ponce de Leon Inlet, is a natural pass to the Atlantic located at the northern end of the lagoon; the other, Haulover Canal, is a man-made passageway at the southern end of the lagoon that leads into the Indian River. Access to or from the Atlantic through Ponce de Leon Inlet is restricted because of a series of islands and small passageways in the northern part of the lagoon. Access to or from the Atlantic through Haulover Canal (completed in 1929) would only be recent, and the nearest outlet to the Atlantic south from Haulover canal is roughly 90–100 km. We also were interested in studying red drum from Mosquito Lagoon because our earlier work (Gold et al., 1993, in press) did not include red drum from the east coast of Florida, an area of potential importance to tests of hypotheses regarding genetic subdivision between red drum from the northern Gulf and the U.S. Atlantic (Gold et al., in press). Finally, adult red drum from Mosquito Lagoon form a large part of the broodstock used by the Florida Department of Natural Resources (FDNR) to supplement and enhance the red drum fishery in Florida waters. The genetic composition of Mosquito Lagoon red drum is thus important to research in stocking hatchery-raised fish.

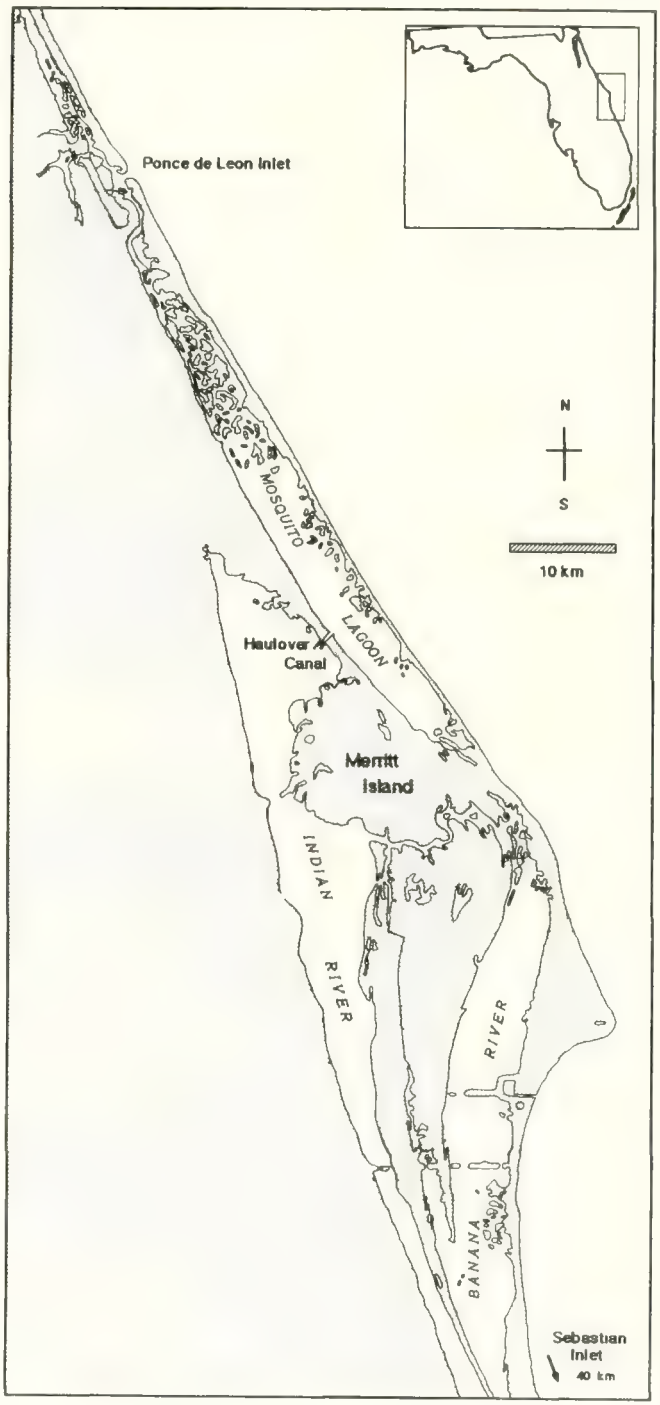

Figure 1

Mosquito Lagoon, east-central Florida, showing Ponce de Leon Inlet and Haulover Canal.

Materials and methods

Red drum were collected from Mosquito Lagoon during fall 1988, spring 1990, and spring 1991. Fish were captured with trammel nets. Tissues (heart, spleen, and muscle) were removed and placed in liquid nitrogen for transport to Texas A&M University where they were stored at –80°C. Ages of all but yearling (age zero) individuals (i.e., specimens less than 300 mm total length) were determined from annuli on otoliths by using methods described in Bumguardner (1991).

Individuals sampled in 1988 (41 total) were surveyed for variation at nine polymorphic allozyme

loci: *ACP-2** (acid phosphatase); *ADA** (adenosine deaminase); *ADH** (alcohol dehydrogenase); *sAAT-1** (aspartate aminotransferase); *EST-1** (esterase); *GPI-B** (glucose phosphate isomerase); and *PEPB**, *PEPD**, and *PEPS** (peptidases). Techniques for vertical starch gel electrophoresis, details of grinding and running buffers, starch composition of gels, protein staining, and interpretation of banding patterns may be found in Bohlmeyer (1989) and Bohlmeyer and Gold (1991). Designation of allelic variants was based on relative mobility to the most common allele (Allele **100*).

All individuals collected (109 total) were assayed for 104 mtDNA restriction sites with 13 restriction enzymes: *Bam*HI, *Bcl*I, *Eco*RV, *Hin*dIII, *Nco*I, *Nsi*I, *Pst*I, *Pvu*II, *Sca*I, *Spe*I, *Stu*I, *Xba*I, and *Xmn*I. Methods used to assay mtDNAs of individual fish may be found in Gold and Richardson (1991). Homology of fragments from single digestions was tested by multiple, side-by-side comparisons. Variant patterns exhibiting only a single band of greater than 15 kb were tested for homology by using double digestions with *Bam*HI as described in Gold and Richardson (1991).

Red drum from Mosquito Lagoon were initially subdivided into year classes and tested for heterogeneity in both allozyme and mtDNA haplotype frequencies. Year classes (number of individuals) were 1985 (17), 1986 (25), 1987 (11), 1988 (7), and 1989 (49). No significant heterogeneity ($P>0.05$) in allozyme or mtDNA haplotype frequencies was found among year classes. Subsequent data analyses employed three test groups: 1) red drum from Mosquito Lagoon; 2) red drum from the northeastern Gulf; and 3) red drum from the Carolina coast. Data for the latter two were taken from Gold et al. (1993, 1994) and represent red drum from the following localities: northeastern Gulf — Apalachicola Bay, Riviera Bay, and Sarasota Bay (west coast of Florida); and Carolina coast — Calibogue Sound, Charleston Bay, and North Inlet (South Carolina), and the Pamlico River and Oregon Inlet (North Carolina). A map showing these localities may be found in Bohlmeyer and Gold (1991). A summary of allele frequencies at the nine polymorphic allozyme loci and the distribution of mtDNA haplotypes in each test group are given in Appendix Tables 1 and 2, respectively.

For allozyme data, tests of Hardy-Weinberg equilibrium expectations and generation of Nei's (1978) unbiased genetic distance were accomplished by using BIOSYS-1 (Swofford and Selander, 1981). Deviations from Hardy-Weinberg expectations were tested by using pooled genotypes and the chi-square statistic with one degree of freedom. Significance testing of allele-frequency differences among test groups was accomplished by using 1) the *G*-statistic (Sokal and Rohlf, 1969) on contingency tables of allele counts and the BIOM-PC program (Rohlf, 1983), and 2) the *V*-statistic (DeSalle et al., 1987) on arcsin, square-root transformed allele frequencies. For mtDNA data, significance testing of mtDNA-haplotype frequency differences was carried out by using the *G*- and *V*-statistics as described above and a Monte Carlo randomization procedure (Roff and Bentzen, 1989). Nucleon diversities and intra- and inter-populational nucleotide sequence diversities were estimated by using equations in Nei and Tajima (1981). Analysis of mtDNA data was facilitated by the Restriction Enzyme Analysis Package (REAP) of McElroy et al. (1992). Significance levels for multiple tests performed simultaneously were adjusted after Cooper (1968).

Results

No significant deviations from Hardy Weinberg equilibrium expectations at any of the nine polymorphic allozyme loci were found following corrections for multiple tests. Two significant deviations were found in uncorrected tests: at *GPI-B** ($P=0.015$) and *PEPS** ($P=0.012$) in the northeastern Gulf. Both deviations appeared to be due to rare homozygotes for low frequency alleles. One new allele (Allele **110* at *EST-1**) was found among Mosquito Lagoon fish at a frequency of 1.2 percent (Appendix Table 1).

Estimates of allozyme variation (Table 1) indicate that red drum from Mosquito Lagoon have fewer

Table 1

Allozyme variation in red drum (*Sciaenops ocellatus*).

Test group	Mean sample size/locus	Mean number of alleles/locus (± SE)	Mean heterozygosity/locus[1] (±SE)
Northeastern Gulf of Mexico	246	3.9 ± 0.9	0.225 ± 0.076
Mosquito Lagoon, Florida	41	2.9 ± 0.6	0.206 ± 0.081
U.S. Carolina Coast	176	3.9 ± 0.9	0.213 ± 0.074

[1] Direct-count estimate.

alleles per locus or lower estimates of mean heterozygosity, or both, than do red drum from the northeastern Gulf and Carolina coast. The differences in genetic variation, however, are non-random across loci. Heterozygosity per locus values among Mosquito Lagoon fish at loci (e.g., *ACP-2**, *ADA**, *ADH**, *sAAT-1**, and *EST-1**) where alternate alleles occurred at frequencies of five percent or greater were equivalent to values among fish from the northeastern Gulf and Carolina coast (data not shown). Differences in heterozygosity per locus values were observed at loci (e.g., *GPI-B**, *PEPB**, and *PEPD**) where alleles occurring in a frequency of one to three percent in northeastern Gulf or Carolina coast fish, or both, were not found among Mosquito Lagoon fish (Appendix Table 1).

Significant heterogeneity ($P<0.05$) in allele frequencies among test groups was found by using the *G*-test at *ADA** ($G=33.92$, df=22, $P\approx0.004$) and *sAAT-1** ($G=13.59$, df=6, $P\approx0.036$). Additional *G*-tests were carried out after pooling alleles whose frequency in any sample was less than 10%. Significant heterogeneity was again found at *ADA** ($G=9.62$, df=4, $P\approx0.048$) and also at *PEPB** ($G=6.86$, df=2, $P\approx0.034$). Examination of allele frequencies at *ADA**, *sAAT-1*, and *PEPB** did not reveal any striking differences among test groups, suggesting that heterogeneity was due to accumulation of small differences in frequencies of rare alleles. At *ADA**, for example, the frequency of Allele **115* was higher among Mosquito Lagoon fish and lower among Carolina coast fish; whereas the frequencies of Alleles **90* and **85* were higher among northeastern Gulf fish (Appendix Table 1). At *sAAT-1** and *PEPB**, slight frequency differences were apparent for Allele **110* (higher in Mosquito Lagoon fish) and Allele **115* (higher in northeastern Gulf fish and absent from Mosquito Lagoon fish), respectively (Appendix Table 1). The observation that *G*-test heterogeneity was due to small, cumulative frequency differences was corroborated by *V*-tests where no significant heterogeneity ($P>0.05$) in allele frequencies was found at any locus following corrections for multiple tests.

MtDNA fragment patterns from single digestions with 13 restriction enzymes generated 36 composite mtDNA haplotypes among fish from Mosquito Lagoon, eleven of which (numbers 114, 134–143) have been found only in Mosquito Lagoon red drum (Appendix Table 2). Estimates of mtDNA variation (Table 2) indicated that nucleon diversity (the probability of any two individuals differing in mtDNA haplotype) was highest in red drum from the northeastern Gulf and lowest in red drum from the Carolina coast; whereas intrapopulational nucleotide sequence diversity (the genetic difference between any two individuals) was greatest among Mosquito Lagoon fish. These estimates of mtDNA variation are among the highest reported to date for a non-clupeid, marine fish species (Richardson and Gold, 1993).

Highly significant heterogeneity in mtDNA-haplotype frequencies among test groups and between pairwise comparisons of test groups were found in both *G*-tests and Monte Carlo bootstrapping (Table 3). These results indicate that all three test groups differ significantly from each other. *V*-tests, carried out on haplotypes found in ten or more individuals (12 haplotypes total), identified six haplotypes (Table 4) that differed significantly among test groups. Genetic distances based on allozymes and mtDNAs (Table 5) indicate that red drum from Mosquito Lagoon are at least as divergent genetically from red drum in the northeastern Gulf and Carolina coast as the latter two are from each other.

Discussion

Tests of heterogeneity clearly indicate that red drum from Mosquito Lagoon differ genetically from red drum in the northeastern Gulf and along the Carolina coast and that at least three subpopulations of red drum occur in U.S. waters. That the genetic differences appear more pronounced in mtDNA than

Table 2

MtDNA variation in red drum (*Sciaenops ocellatus*).

Test group	Number of individuals	Number of haplotypes	Nucleon diversity	Nucleotide sequence diversity (± SD)[1]
Northeastern Gulf of Mexico	247	49	0.947	0.557 ± 0.298
Mosquito Lagoon, Florida	109	36	0.912	0.597 ± 0.321
U.S. Carolina Coast	174	43	0.904	0.560 ± 0.351

[1] Values are in percent. Standard deviations are used instead of standard errors because of the large number of pairwise comparisons used to generate mean values.

Table 3

Results of tests for heterogeneity in mtDNA haplotype frequencies among red drum (*Sciaenops ocellatus*) from the northeastern Gulf of Mexico, Mosquito Lagoon, Florida, and the U.S. Carolina coast.

Test group	Results of *G*-tests		*P*-value from Monte Carlo randomizations
	G-score	*P*-value	
Northeastern Gulf vs. Mosquito Lagoon vs. Carolina Coast	159.5	<0.001[1]	<0.001
Northeastern Gulf vs. Mosquito Lagoon	73.9	<0.001[2]	<0.001
Northeastern Gulf vs. Carolina Coast	76.2	<0.001[3]	<0.001
Mosquito Lagoon vs. Carolina Coast	66.2	<0.001[4]	0.006

Degrees of freedom in *G*-tests: 48[1], 18[2], 19[3], and 27[4].

Table 4

Frequency[1] of six significantly heterogeneous mtDNA haplotypes of red drum (*Sciaenops ocellatus*) in the northeastern Gulf of Mexico, Mosquito Lagoon, Florida, and the U.S. Carolina coast.

Haplotype	Northeastern Gulf (n=247)	Mosquito Lagoon (n=109)	Carolina Coast (n=174)	Probability value from *V*-test[2]
8	13.3	23.8	10.3	≈0.010
9	7.7	13.8	26.4	<0.001
11	9.3	1.8	7.5	≈0.019
12	0.0	7.3	3.4	<0.001
21	4.4	0.0	0.6	≈0.004
29	4.0	0.0	1.7	≈0.021

[1] Values are in percent.
[2] After DeSalle et al. (1987).

in (presumed) nuclear-coding genes is not surprising, given that mtDNA is expected to be at least four times more sensitive to population substructuring (Birky et al., 1983; Templeton, 1987). Because previous studies (Gold et al., 1993, in press) found no evidence of genetic heterogeneity among red drum from eleven estuaries or bays in the northern Gulf or among red drum from five estuaries or bays along the Carolina coast, red drum from Mosquito Lagoon are unusual in representing a genetically distinct red drum subpopulation existing within a single bay or estuary.

Campton (1992)[4] examined red drum from Mosquito Lagoon for allelic variation at several allozyme loci and found genetic homogeneity among red drum from Mosquito Lagoon, the northern Gulf, and the Carolina coast. He suggested that our initial study (Bohlmeyer and Gold, 1991) of allozyme variation among northern Gulf and Carolina coast red drum did not account for temporal variation among samples within localities. Our subsequent studies (and this one), however, have included temporal sampling of variation in *both* allozymes and mtDNA and have demonstrated that weak (but significant) genetic heterogeneity exists (Gold et al., 1993, in press). Sampling error associated with specimen procurement in varying time and space may account for the different results obtained in Campton's (1992)[4] study and this one. However, in Campton's (1992)[4] study, the total *G*-statistic, obtained by summing individual *G*-values and their associated degrees of freedom, was significant at the 0.01 level. This suggests the existence of spatial or temporal genetic heterogeneity, or both, among the localities sampled.

Genetic differentiation of red drum in Mosquito Lagoon is consistent with the hypothesis that red drum in Mosquito Lagoon represent a self-contained, at least partially isolated subpopulation. Three lines of evidence support this hypothesis. First, genetic differences between red drum from Mosquito Lagoon and red drum sampled elsewhere involve frequencies of alleles at two or three putative nuclear-gene loci and frequencies of at least six mtDNA haplotypes. Differentiation of several, presumably independent and selectively-neutral, genetic markers suggests a genome-wide effect related to at least partial isolation and reduced gene flow (Wright, 1978; Hartl and Clark, 1989). Second, inferred nuclear-gene alleles present in low frequency in red drum sampled outside of Mosquito

[1] Campton, D. E. 1992. Gene flow estimation and population structure of red drum (*Sciaenops ocellatus*) in Florida. Final Rep. Coop. Agrmt. No. 14–16–009–1522, U.S. Fish & Wildl. Serv., Natl. Fish. Res. Cntr., 7920 N.W. 71st St., Gainesville, FL.

Table 5

Matrix of Nei's (1978) unbiased genetic distance based on allozymes (upper diagonal) and Nei and Tajima's (1981) corrected interpopulational nucleotide sequence divergence based on mtDNAs (lower diagonal) among red drum (*Sciaenops ocellatus*) from the northeastern Gulf of Mexico, Mosquito Lagoon, Florida, and the U.S. Carolina coast. Interpopulational nucleotide sequence divergence values are in percent.

	Northeastern Gulf	Mosquito Lagoon	Carolina Coast
Northeastern Gulf	—	0.000	0.001
Mosquito Lagoon	0.006	—	0.002
Carolina Coast	0.006	0.009	—

Lagoon were not found in red drum from Mosquito Lagoon; whereas one inferred allele and eleven mtDNA haplotypes were unique to red drum from Mosquito Lagoon. The distribution of low frequency nuclear-gene alleles and mtDNA haplotypes is consistent with reduced gene flow concomitant with allele-frequency drift expected in isolated subpopulations. Finally, both females with ovaries containing postovulatory follicles and spawned red drum eggs have been documented in Mosquito Lagoon (Murphy and Taylor, 1990; Johnson and Funicelli, 1991), clearly indicating that red drum spawn within the system.

Assuming red drum in Mosquito Lagoon represent a partially isolated, self-contained subpopulation, one question of interest is how long the subpopulation has been semi-isolated. Geological evidence (Mehta and Brooks, 1973, cited from Johnson and Funicelli, 1991) indicates that several tidal inlets once connected Mosquito Lagoon to the Atlantic, the last of which is estimated to have closed about 1,500 years ago. Assuming some variation in the geological estimate, this date does not differ substantially from an estimate of 2,900 ± 1,550 (SD) years based on 1) a corrected interpopulational nucleotide sequence divergence (between red drum in Mosquito Lagoon and red drum elsewhere) of 0.0058 ± 0.0031 (SD) percent, and 2) an evolutionary rate for vertebrate mtDNA of 0.01 substitutions/bp/lineage/Myr (Brown et al., 1979; Wilson et al., 1985). Given ongoing debates about molecular clocks, the correspondence between the two temporal estimates is noteworthy.

Because the genetic distinctness of Mosquito Lagoon red drum appears to stem largely from physical isolation, the biological reasons for subdivision between red drum in the northern Gulf and those along the Carolina coast remain unknown. Possible reasons for this subdivision could include 1) current patterns between the Gulf and U.S. Atlantic, 2) absence of suitable near-shore habitats along the southeastern coast of Florida, or 3) differences in biogeographic provinces (Gold et al., 1993, in press). Similar genetic discontinuities between U.S. Atlantic and Gulf coast fauna have been described by Avise and co-workers (reviewed in Avise, 1992). Their hypothesis is that the concordant phylogeographic patterns provide evidence of similar vicariant histories that are tentatively related to episodic changes in environmental conditions during the Pleistocene (Avise, 1992). The relative inaccessibility of Mosquito Lagoon suggests that sampling red drum from north or south of Mosquito Lagoon may be more informative for testing hypotheses regarding phylogeographic subdivision between the northern Gulf and the U.S. Atlantic.

A last point to consider is the use of Mosquito Lagoon red drum as broodstock for stock enhancement programs. It could be argued that red drum from Mosquito Lagoon differ genetically from red drum sampled elsewhere (e.g., the northeastern Gulf) and should be used only for stock enhancement at localities where no genetic differences exist. Alternatively, it could be argued that the genetic distinctiveness of red drum in Mosquito Lagoon is relatively small and possibly inconsequential. This follows from the observation that the documented genetic difference between red drum in Mosquito Lagoon and red drum sampled elsewhere is considerably less than that, on average, among races of man (Cann et al., 1987). One other consideration might be to cross red drum from Mosquito Lagoon with red drum from elsewhere (e.g., the northeastern Gulf) in order to increase performance from potential heterotic effects.

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Literature cited

Avise, J. C.
1992. Molecular population structure and the biogeographic history of a regional fauna: a case history with lessons for conservation biology. Oikos 63:62–76.

Birky Jr., C. W., T. Maruyama, and P. Fuerst.
1983. Mitochondrial DNAs and phylogenetic relationships. *In* S. K. Dutta (ed.), DNA systematics, p. 107–137. CRC Press, Boca Raton, FL.

Bohlmeyer, D. A.
1989. A protein electrophoretic analysis of population structure in the red drum (*Sciaenops ocellatus*). M.S. thesis, Texas A&M University, College Station, TX.

Bohlmeyer, D. A., and J. R. Gold.
1991. Genetic studies in marine fishes. II: A protein electrophoretic analysis of population structure in the red drum *Sciaenops ocellatus*. Mar. Biol. 108:197–206.

Brown, W. M., M. George Jr., and A. C. Wilson.
1979. Rapid evolution of animal mitochondrial DNA. Proc. Natl. Academy Sci. (USA) 76:1967–1971.

Bumguardner, B. W.
1991. Marking subadult red drums with oxytetracycline. Trans. Am. Fish. Soc. 120:537–540.

Cann, R. L., M. Stoneking, and A. C. Wilson.
1987. Mitochondrial DNA and human evolution. Nature 325:31–36.

Cooper, D. W.
1968. The significance level in multiple tests made simultaneously. Heredity 23:614–617.

DeSalle, R., A. Templeton, I. Mori, S. Pletscher, and J. S. Johnston.
1987. Temporal and spatial heterogeneity of mtDNA polymorphisms in natural populations of *Drosophila mercatorum*. Genetics 116:215–233.

Gold, J. R., and L. R. Richardson.
1991. Genetic studies in marine fishes. IV: An analysis of population structure in the red drum (*Sciaenops ocellatus*) using mitochondrial DNA. Fish. Res. 12:213–241.

Gold, J. R., L. R. Richardson, C. Furman, and T. L. King.
1993. Mitochondrial DNA differentiation and population structure in red drum (*Sciaenops ocellatus*) from the Gulf of Mexico and Atlantic Ocean. Mar. Biol. (In press.)

Gold, J. R., T. L. King, L. R. Richardson, D. A. Bohlmeyer, and G. C. Matlock.
In press. Genetic studies in marine fishes. VII: Allozyme differentiation within and between red drum (*Sciaenops ocellatus*) from the Gulf of Mexico and Atlantic Ocean. J. Fish Biol. 116:175–185.

Hartl, D. L., and A. G. Clark.
1989. Principles of population genetics, 2nd ed. Sinauer Assoc., Inc., Sunderland, MA.

Johnson, D. R., and N. A. Funicelli.
1991. Spawning of the red drum in Mosquito Lagoon, east-central Florida. Estuaries 14:74–79.

Matlock, G. C.
1984. A basis for the development of a management plan for red drum in Texas. Ph.D. diss., Texas A&M University, College Station, TX.

McElroy, D., P. Moran, E. Bermingham, and I. Kornfield.
1992. REAP-The Restriction Enzyme Analysis Package. J. Hered. 83:157–158.

Mehta, A. J., and H. K. Brooks.
1973. Mosquito Lagoon barrier beach study. Shore and Beach 41:27–34.

Mercer, L.
1984. A biological and fisheries profile of red drum, *Sciaenops ocellatus*. Spec. Sci. Rep. 41, North Carolina Dep. Nat. Resour. Community Dev., Div. Mar. Fish., Raleigh, NC.

Murphy, M. D., and R. G. Taylor.
1990. Reproduction, growth, and mortality of red drum, *Sciaenops ocellatus*, in Florida. Fish. Bull. 88:531–542.

Nei, M.
1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590.

Nei, M., and F. Tajima.
1981. DNA polymorphism detectable by restriction endonucleases. Genetics 97:145–163.

Overstreet, R. M.
1983. Aspects of the biology of the red drum, *Sciaenops ocellatus*, in Mississippi. Gulf Res. Rep. (Suppl.) 1:45–68

Richardson, L. R., and J. R. Gold.
1993. Mitochondrial DNA variation in red grouper (*Epinephelus morio*) and greater amberjack (*Seriola dumerili*) from the Gulf of Mexico. ICES J. Mar. Sci. 50:53–62.

Roff, D. A., and P. Bentzen.
1989. The statistical analysis of mitochondrial polymorphisms: chi-square and the problem of small samples. Mol. Biol. Evol. 6:539–545.

Rohlf, F. J.
1983. BIOM-PC: a package of statistical programs to accompany the text BIOMETRY. W. H. Freeman & Co., San Francisco, CA.

Sokal, R. R., and F. J. Rohlf.
1969. Biometry. The principles and practice of sta-

tistics in biological research. W. H. Freeman & Co., San Francisco, CA.

Swofford, D. L., and R. B. Selander.

1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72:281–283.

Templeton, A. R.

1987. Genetic systems and evolutionary rates. *In* K. F. S. Campbell and M. F. Day (eds.), Rates of evolution, p. 218–234. Australian Acad. Sci., Canberra.

Wilson, A. C., R. L. Cann, S. M. Carr, M. George Jr., U. B. Gyllensten, K. M. Helm-Bychowski, R. G. Higuchi, S. R. Palumbi, E. M. Prager, R. D. Sage, and M. Stoneking.

1985. Mitochondrial DNA and two perspectives on evolutionary genetics. Biol. J. Linnaean Soc. 26:375–400.

Wright, S.

1978. Evolution and the genetics of populations. Univ. Chicago Press, Chicago, IL.

Appendix Table 1

Allele frequencies at nine polymorphic loci among red drum (*Sciaenops ocellatus*) from the northeastern Gulf of Mexico, Mosquito Lagoon, Florida, and the U.S. Carolina coast.

Locus allele	Northeastern Gulf of Mexico[1]	Mosquito Lagoon, Florida	U.S. Carolina coast[1]
*ACP-2**			
*125	0.002	0.012	0.000
*115	0.087	0.073	0.063
*100	0.911	0.915	0.937
(*n*)	(246)	(41)	(175)
*ADA**			
*150	0.000	0.012	0.003
*130	0.036	0.024	0.028
*125	0.315	0.354	0.372
*118	0.006	0.000	0.003
*115	0.081	0.122	0.028
*113	0.002	0.000	0.003
*110	0.061	0.012	0.060
*100	0.443	0.452	0.469
*90	0.010	0.000	0.003
*85	0.024	0.000	0.003
*78	0.000	0.000	0.000
*75	0.018	0.024	0.028
*65	0.004	0.000	0.000
(*n*)	(247)	(41)	(176)
*ADH**			
*–100	0.508	0.451	0.566
*–75	0.458	0.525	0.391
*–50	0.028	0.012	0.020
*–20	0.006	0.012	0.023
(*n*)	(246)	(41)	(175)
*sAAT-1**			
*120	0.000	0.012	0.017
*110	0.134	0.171	0.120
*100	0.856	0.817	0.854
*90	0.010	0.000	0.009
(*n*)	(242)	(41)	(175)
*EST-1**			
*110	0.000	0.012	0.000
*100	0.911	0.915	0.898
*95	0.089	0.073	0.102
(*n*)	(246)	(41)	(176)
*GPI-B**			
*–110	0.004	0.000	0.003
*–100	0.976	1.000	0.971
*–50	0.020	0.000	0.026
(*n*)	(247)	(41)	(176)
*PEPB**			
*115	0.022	0.000	0.006
*100	0.974	1.000	0.991
*85	0.004	0.000	0.003
(*n*)	(247)	(41)	(176)
*PEPD**			
*115	0.002	0.012	0.009
*100	0.968	0.988	0.968
*85	0.030	0.000	0.020
*75	0.000	0.000	0.003
(*n*)	(247)	(41)	(176)
*PEPS**			
*105	0.040	0.024	0.023
*100	0.958	0.976	0.977
*95	0.002	0.000	0.000
(*n*)	(247)	(41)	(176)

[1] Data are from Gold et al. (in press).

Appendix Table 2

Distribution of mtDNA haplotypes among red drum (*Sciaenops ocellatus*) from the northeastern Gulf of Mexico, Mosquito Lagoon, Florida, and the U.S. Carolina coast.

Haplotype	Composite mtDNA digestion pattern[1]	Northeastern Gulf of Mexico[2]	Mosquito Lagoon, Florida	U.S. Carolina coast[2]	Haplotype	Composite mtDNA digestion pattern[1]	Northeastern Gulf of Mexico[2]	Mosquito Lagoon, Florida	U.S. Carolina coast[2]
1	ABAAAAAAAAAAA	19	4	10	56	AGAAAAAAAAAAA	—	—	1
2	ABCCAAAAAAAAA	10	6	3	57	AAAAAABAAAEAA	—	—	1
3	ABBACAAAAAAAA	11	1	10	58	BBAAAFAAAAAAA	3	—	—
4	EAAAAABAAAAAA	1	—	—	60	FBBAAAAAAACAA	—	—	1
5	BAAAACBAAAAAA	1	—	—	61	AAAAAAAADAAAA	—	—	1
6	CBAAAAAAAAAAA	2	1	1	62	BBBAAAAAAAAAA	—	—	1
7	AAABAAAAAAAAA	7	1	—	64	AAAEAABAAAAAA	5	—	—
8	AAAAAABAAAAAA	33	26	18	66	BBADAAAAAAAAA	—	—	1
9	BAAAAAAAAAAAA	19	15	46	68	BBAEAAAAAAAAA	1	—	—
10	BBAAAAAAAAAAA	9	2	4	69	AFAAAABAAAAAA	4	—	—
11	AAAAAAAAAAAAA	23	2	13	70	ACAAAAAACAAAA	1	—	—
12	CBAAAABAAAAAA	—	8	6	76	BAAAAAAAABAAA	2	—	—
13	ABCAAACAAAAAA	1	—	4	77	ABAAAGFAAAAAA	1	—	—
14	BBFAAAAAAABAB	—	—	4	82	ABAAAAFAAAAAA	4	—	—
15	AAAAAABACAAAA	—	1	2	89	BIAAAAAAAAAAA	—	—	1
16	ACAAAAAAAAAAA	6	2	4	90	BAAAAAGAEAAAA	—	1	1
18	ABAACAAAAAAAA	5	2	1	91	AAAAAAABAAAAA	—	—	1
19	BBAAADAAAAAAA	—	2	5	92	ABBAFAAAAACAA	—	—	1
20	ABBAAAAAAACAA	—	3	2	93	AAAFGAAAEAAAA	1	—	—
21	BABAAAAAAAAAA	11	—	1	94	AAAAAABAAAADA	1	—	—
22	BAAAAABAAAAAA	4	1	2	95	BAAAAHAAAAAAC	2	—	—
23	AAAABAAAAAAAA	17	6	8	96	BCAAAAAAAAAAA	1	—	—
24	AAAAAAAAAAAAC	5	2	1	97	HBAAAAAAAAAAA	1	—	—
25	ADCCAAAAAAAAA	2	—	1	98	BAAABAAAAAAAA	1	—	—
26	BABABAAAAAAAA	3	1	1	99	BBBAAAAAAAFAA	1	—	—
27	AACCAAAAAAAAA	—	5	1	100	AAIAAABAAAAAA	1	—	—
28	ABAADAAAAAAAA	—	2	2	101	ABCCAAFAAAAAA	1	—	—
29	AAAAABABAAAAA	10	—	3	106	AAAAIAAAAAAAC	1	—	
31	DBCAAAAAAAAAA	1	—	—	107	BAAAABABAAAAA	2	—	—
35	ABBAAAAAAAAAA	—	2	4	114	ACBAAAAAAAAAA	—	1	—
36	ABADAAAAAAAAA	1	—	1	121	ABADAAAADAAAA	1	—	—
45	BABAAABAAAAAA	2	—	—	134	AAAAGABAAAAAA	—	1	—
46	ABEAAAAAAAAAA	1	1	—	135	BBJAADAAAAAAA	—	1	—
47	BBAAAFAAEAAAA	2	—	—	136	BBADAAABAAAAA	—	1	—
48	AAEAAAAAAAAAA	1	—	—	137	BBAAAAACAABAA	—	1	—
49	CBBAAAAAAAAAA	3	—	—	138	BBAAAAAAAABAB	—	1	—
50	BBHAAAAAAABAB	—	—	1	139	AAACAAAAAAAAA	—	1	—
51	ABCAAAAAAAAAA	—	1	1	140	ABACAAAAAAAAA	—	1	—
52	BBAAAAACAABAB	—	—	1	141	AACABAAAAAAAA	—	1	—
53	ABBAAAAAAAFAA	2	—	1	142	AACAAABAAAAAA	—	1	—
54	BAAEAAAAAAAAA	—	—	1	143	ABAAGAAAAAAAA	—	1	—
55	AHCCAAAAAAAAA	—	—	1					

[1] Letters (from left to right) are digestion patterns for: *Nco*I, *Bcl*I, *Sca*I, *Pvu*II, *Spe*I, *Xba*I, *Xmn*I, *Hin*dIII, *Stu*I, *Bam*HI, *Eco*RV, *Pst*I, and *Nsi*I. Details regarding fragment sizes of individual digestion patterns are available upon request.

[2] Data are from Gold et al. (1993).

Distribution and abundance of copepod nauplii and other small (40–300 μm) zooplankton during spring in Shelikof Strait, Alaska*

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Abstract.—Microzooplankton retained by a 41-μm mesh was sampled along a 50-km transect in the Shelikof Strait between Kodiak Island and the Alaska Peninsula. We sampled once each year during spring (April–May) 1985–1989 using Niskin bottles closed at 10-m depth intervals. Sampling was conducted near the time and place of peak hatching of walleye pollock (*Theragra chalcogramma*) larvae. We examined horizontal and vertical patterns of abundance of potential prey organisms, especially copepod nauplii, and described these patterns with respect to the oceanography of the Strait. Hydrography, nutrients, chlorophyll-*a* and net zooplankton data also were collected and were used to help interpret the microzooplankton patterns. Copepod nauplii composed from 46 to 82% of all organisms in the formalin-preserved samples. Eggs (3–35%), rotifers (up to 14%) and loricate tintinnids (up to 11%) were the next most abundant taxa. The abundance of microzooplankton varied greatly across the Strait and, for copepod nauplii, had maxima associated with the Alaska Coastal Current. A mesoscale feature in the coastal current appeared to influence the distribution of microzooplankton and may affect feeding conditions for larval walleye pollock. Significant differences in abundance of copepod eggs and nauplii were detected between some transects. The integrated, 0-60 m depth, across-strait average abundance of copepod nauplii varied from a low of 5.8×10^3 m^{-2} (sampled in 1985) to a high of 17.6×10^3 m^{-2} (1987). The maximum concentration found in these same transects varied from 18 to 144 L^{-1}, respectively. Between 60 and 70% of the nauplii sampled were of a size (>125 μm total length) composing approximately 98% of the naupliar diet of larval walleye pollock in spring.

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The high mortality rate of marine fish larvae is attributed to high rates of predation (Moller, 1984; Bailey and Houde, 1989), sensitivity to feeding conditions (Theilacker and Watanabe, 1989) and interactions between these factors (Houde, 1987; Purcell and Grover, 1990). The larvae of temperate fishes often occur during spring, when planktonic production is in early stages of its annual cycle and is easily disrupted or delayed by adverse conditions. Also, larvae have small search volumes and generally small energy reserves (Bailey and Houde, 1989). Thus, a spatial or temporal "match" or "mismatch" between the demand for larval food and its availability seems intuitively likely and has been the subject of much research (e.g., Lasker, 1981; Buckley and Lough, 1987; Cushing, 1990). The quest to quantify feeding relationships has led to continuing efforts to reduce container effects in experimental studies (Gamble and Fuiman, 1987; McKenzie et al., 1990), to improve the sensitivity of physiological measurements (e.g., Buckley et al., 1990), to understand the small-scale distribution of prey in the field (Owen, 1989), and to understand the role of mixing in enhancing or retarding interactions between predator and prey (Rothschild and Osborne, 1988; Davis et al., 1991). In the ocean, feeding takes place in a complex spatial array of biological and physical conditions. Any study of rate-influencing processes that affect larvae must take into account the distribution of these conditions in order to understand effects at the population level.

In this paper we examine the springtime community of small zooplankton, primarily copepod nauplii, that may be prey for larval walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska (Fig. 1), and we report on the distribution and abundance of these organisms with respect to oceanographic conditions. A large population of walleye pollock spawns in the Strait in late March and early April, forming dense aggregations of planktonic eggs in the deepest part of the sea valley between Kodiak Island and the Alaska Peninsula. Hatching occurs from middle or late April through early May (Kendall et al., 1987; Incze et al., 1989; Yoklavitch and Bailey, 1990). While the eggs remain mostly below 150 m, larvae

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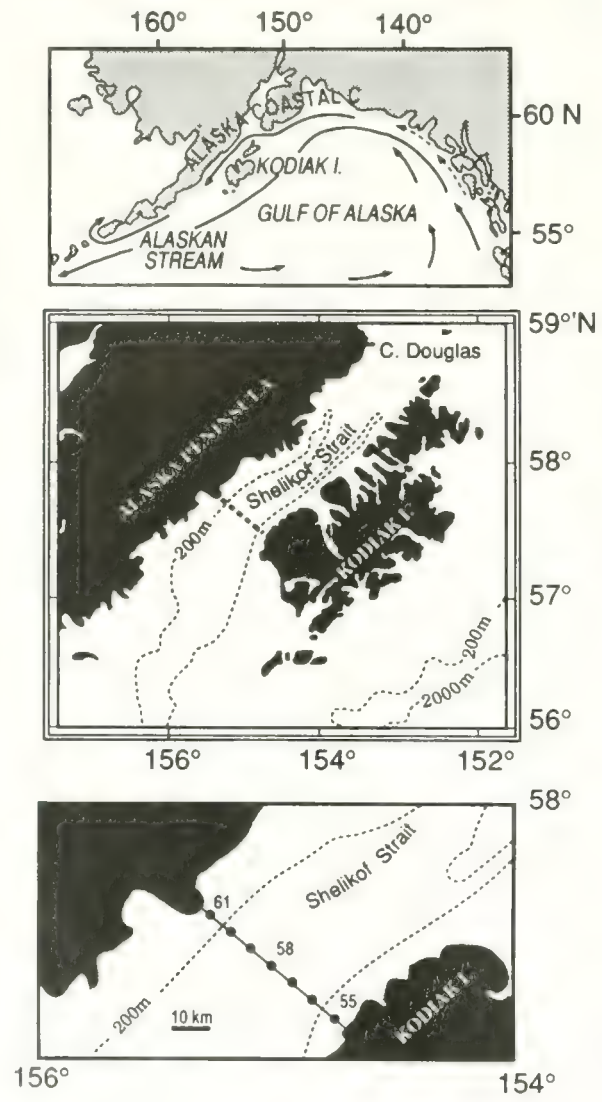

Figure 1

Top panel shows location of the study area and a generalized scheme of the surface circulation. Middle and bottom panels show Shelikof Strait and the sampling transect. Stations are numbered consecutively beginning with 55 near the Kodiak Island shore; only the end and middle stations are labeled.

are found primarily in the upper 50 m (Kendall et al., 1993[1]) and have been shown to prey heavily on copepod nauplii during the first several weeks of development (Dagg et al., 1984; Kendall et al., 1987; Canino et al., 1991).

The upper water column of Shelikof Strait consists of at least three distinct water types (Reed and Schumacher, 1989). A cold, slightly freshened, turbid coastal water band of narrow width (<10 km) remains near the Alaska Peninsula (northern) side of the Strait. This water receives its signature from glacial melt-waters draining into Cook Inlet at the northern end of the Strait and thus varies seasonally in volume. A second water type is encompassed in the Alaska Coastal Current (ACC), part of a baroclinic current running more or less continuously along 1000 km of the Alaskan south coast. The ACC flows from northeast to southwest in a band approximately 20 km wide through the middle portion of the Strait, but it has a highly variable current structure marked by numerous baroclinic instabilities (Mysak et al., 1981; Vastano et al., 1992). In the vertical, the southward flow of the ACC induces an opposite bottom flow of more saline, nutrient rich water that enters the sea valley at the shelf edge south of the study area (Fig. 1; see Reed et al., 1987). A third water type is made up of waters from a mixture of sources, including outer shelf and oceanic intrusions. Most of this water enters from the north and flows the length of the Strait along Kodiak Island, but current meter measurements and satellite imagery show that water sometimes enters from the south (Schumacher, 1991[2]).

The work reported here was undertaken as part of a multi-disciplinary program (Fisheries Oceanography Coordinated Investigations: FOCI) aimed at understanding the influence of environmental factors on the early life history of walleye pollock spawned in the Strait (Schumacher and Kendall, 1991). An extensive grid of sampling stations occupied in early May 1985, the first year of the program, showed that the spring bloom of large diatoms did not occur homogeneously throughout the Strait. Rather, in that year, large diatoms bloomed first in a band which occupied the longitudinal mid-portion of the Strait (Incze, unpubl. observ.). Hydrographic data show that this feature was in the ACC, which had at that time a shallower upper mixed layer than elsewhere in the Strait. It seemed likely, therefore, that conditions affecting the feeding and growth of larval walleye pollock would be subject to dynamics of the ACC and would differ across the Strait as well as through time. As part of the research program, a standard across-strait transect was established near the southern end of the Strait proper (about halfway up the sea valley: Fig. 1). This transect has been sampled with a CTD (Conductivity, Temperature, Depth) as often as ship and research schedules have permitted. Biological sam-

[1] A. W. Kendall Jr., L. S. Incze, P. B. Ortner, S. R. Cummings, and P. K. Brown. 1993. The vertical distribution of eggs and larvae of walleye pollock in Shelikof Strait, Gulf of Alaska. Submitted to Fish. Bull.

[2] J. Schumacher. 1991. Pacific Marine Environmental Laboratory, Seattle, WA, unpubl. data.

pling begins along this transect near the time of larval hatching each spring and proceeds down-current (westward) over time. In this paper we report on across-shelf patterns of abundance and vertical distribution of copepod nauplii and other small zooplankton from 1985 through 1989 and relate these patterns to hydrographic conditions, chlorophyll concentrations, and distributions of selected taxa of adult female copepods.

Materials and methods

For convenience, we use the term microzooplankton to refer to small zooplankton captured and preserved by methods described below. Hydrography, nutrients, and microzooplankton were sampled with a CTD and rosette sampler along a transect of stations across Shelikof Strait, Alaska, during spring from 1985 through 1989 (Fig. 1) (sampling dates are listed in Table 2). Hydrographic (CTD) data were obtained near bottom at 7 stations at 7–km intervals and were processed to give 1–m averaged data of salinity, temperature and density. Nutrients were sampled at five or more stations on the transect by removing water samples from 10–L Niskin bottles tripped at standard depths of 10, 20, 30, 50, 75, and 100 m; below this depth we sampled with lower resolution, generally at 50–m intervals, plus a sample near bottom. Nutrient concentrations were determined after the cruise by using standard autoanalyzer techniques on frozen samples (Whitledge et al., 1981[3]). Chlorophyll data were obtained from nutrient sampling depths in the upper 100 m in 1988 and 1989. Analyses were conducted on board the vessel following methods of Yentsch and Menzel (1963) as modified by Phinney and Yentsch (1985) with 0.45–μm Millipore HA acetate filters. Microzooplankton was sampled from Niskin bottles were tripped at 10–m intervals from 0 to 60 m in 1985 and from 10 to 60 m in other years. We used the same bottles as for nutrient and chlorophyll samples for those depths which were common to all. The number of stations sampled varied over the years, beginning in 1985 with stations 55, 58, and 61. In 1986 and 1987 we included station 60. In 1988 we sampled all seven stations along the transect, and in 1989 we sampled all except station 57.

Niskin bottles were sampled for nutrients and chlorophyll when called for; the remaining contents of the bottles were filtered through small (6 × 18 cm) conical nets made of 41–μm mesh nylon netting. Material retained on the netting was flushed into 4–ounce (120 mL) glass jars by using 0.45–μm filtered seawater and was preserved in a final solution of 5% formalin:seawater. Larger zooplankton was sampled at all seven stations by using 60–cm diameter bongo samplers equipped with 333–μm mesh nets and towed in double-oblique fashion from the surface to about 10 m off bottom. From 1986 onward, a 20–cm bongo sampler with 150–μm mesh nets was attached to the towing wire 1 m above the larger sampler to try to improve on the sampling of smaller copepods. Properties of each tow were monitored by time, wire angle from the towing block, mechanical flowmeters mounted across the mouth of each net, and a bathykymograph attached to the bridle of the large bongo.

In the laboratory, each microzooplankton sample was filtered onto a 41–μm mesh sieve, stained overnight in Rose Bengal, transferred to a 10–mL scintillation vial and examined in approximately 2–mL aliquots. Microzooplankton was analyzed by using a stereo dissecting microscope equipped with an image analysis system consisting of a high-resolution video camera and computer software to make measurements and record data (Incze et al., 1990). The microscopist made identifications, placing each organism into one of thirteen categories (Table 1), and directed the orientation of measurements. Copepod nauplii were measured for total length (TL) and maximum width. Total length was the carapace length ("prosome"), plus the abdomen ("urosome") when present. The latter section often was curled beneath the carapace, necessitating measurement along a curved line. We measured the diameter of eggs and only the total body length of all other organisms. In most cases the entire sample was analyzed, but 25% of the original sample sometimes provided adequate counts, which we established as at least 50 nauplii per sample. Subsampling was done by increasing the stored sample volume to 200 mL, dividing as necessary, then recondensing the material for examination. Subsampling was checked for accuracy by completely analyzing both half-portions from 30 samples. Final counts of microzooplankton were corrected for the subsampling fraction and for differences in the original volume of water filtered and are presented as number of organisms per liter. Integrated abundances (No. m^{-2}) were estimated for the upper 60 m of the water column by using a trapezoidal algorithm.

Vertical and horizontal patterns of microzooplankton distribution were plotted by using an inverse distance gridding technique ("Surfer", Golden Software, Inc., Golden, CO) with a grid size

[3] Whitledge, T. E., S. C. Molloy, C. J. Patton, and C. D. Wirick. 1981. Automated nutrient analyses in seawater. Tech Rep. No. BNL-51398, Brookhaven Natl. Lab., Upton, NY.

Table 1

(**A**) Composition of microzooplankton in Shelikof Strait during spring, expressed as a percent of total organisms counted. Hyphens indicate values greater than zero but less than 2%; non-zero values shown are rounded to nearest whole number. Shed ovisacs are from *Oithona* spp.; "Other" includes infrequent and unidentified organisms. (**B**) Vertically integrated abundances of organisms are averaged across Shelikof Strait for each year; "All other" refers here to all categories from (A) combined except for those specifically listed.

A Percent composition

Category	1985	1986	1987	1988	1989
Copepod nauplii	50	46	54	82	76
Other nauplii	—	—	—	—	—
Invertebrate eggs	25	35	13	3	4
Ovisacs	3	—	—	2	—
Copepods	9	2	—	4	3
Euphausiids	—	0	—	0	0
Rotifers	—	7	14	—	4
Tinitinnids	2	—	11	—	—
Larvaceans	—	3	0	—	—
Polychaetes	—	—	—	—	—
Echinoderms	—	—	—	—	—
Foraminifera	—	—	—	—	—
Other	8	3	4	5	3

B Average integrated abundance (1000s m^{-2}) from 0–60 m

Copepod nauplii	5.8	13.9	17.6	9.4	9.6
Invertebrate eggs	3.0	10.4	3.6	0.4	0.6
All other	4.6	5.7	8.6	1.9	2.6
Total	13.3	30.0	29.8	11.8	12.8

set at 25 units in both the X and Y directions. The same technique was used for contouring CTD and nutrient data. A subset of contours from all three data types was compared by inspection to the original input data to look for artifacts caused by the contouring software. Integrated abundances of nauplii across the Strait were compared for the four years which had late April–early May sampling (1985, '86, '88, '89). Data were taken from those stations (#55, 58, 61) sampled every year in the series and were compared by using a non-parametric two-way analysis of variance (ANOVA) on ranks (also referred to as the Quade test: Conover, 1971). A multiple comparison based on ranks (Conover, 1971) was applied when the ANOVA showed statistically significant differences.

We used the estimated abundances of adult female copepods (No. m^{-2}) from the oblique bongo tows to consider possible sources of planktonic eggs and nauplii sampled in our study. Data are from a database being used to describe spatial and interannual patterns of major zooplankton taxa (FOCI Database, National Marine Fisheries Service, Seattle); subsampling and counting followed standard procedures and are detailed in a series of five reports (e.g., Siefert and Incze, 1991[4]). The relative contribution of each taxon to the standing stock of planktonic copepod eggs and early nauplii was estimated by using egg production rates reported in the literature or from unpublished data. This is simplistic, because it ignores changes in egg and naupliar concentrations as a function of birth rate, development time, and mortality, all of which may vary considerably. However, the calculations provide a rough evaluation of potential sources of nauplii in Shelikof Strait. Sizes of eggs and early nauplii (e.g., Nauplius I [NI]) were used when reports were found. We used the following information: *Calanus marshallae* (eggs 175–185 µm, fecundity 12 eggs d^{-1} [Runge, 1990[5]]; *Calanus pacificus* (eggs ca. 160 µm, fecundity 38 eggs d^{-1} [Runge, 1984]; NI ca. 220 µm CL [Fulton 1972]); *Metridia pacifica* (eggs 150 µm [Runge, 1990[6]]; fecundity 2.5 eggs d^{-1} [Batchelder and Miller, 1989]); *Pseudocalanus* spp. (eggs ca. 110–130 µm retained in ovisacs [Frost, 1987]; fecundity 4 eggs d^{-1} [Dagg et al., 1984; Paul et al., 1990]; NI ca. 180 µm CL [Fulton, 1972]). Jeffry Napp[7] and Kenric Osgood[8] both have found that *Metridia pacifica* held in the laboratory may produce eggs at higher rates, and they suggest that the population average at times may be several times greater than the rate given above.

Results

In this section we designate different transects by the year in which they were sampled but do not mean to imply that the differences necessarily were interannual. We address this distinction in the discussion section.

Nitrate concentrations in bottom waters were highest in 1985, 1988, and 1989 (>25 µg-at L^{-1} com-

[4] Siefert, D. L. W., and L. S. Incze. 1991. Zooplankton of Shelikof Strait, Alaska, April and May 1989: data from Fisheries Oceanography Coordinated Investigations (FOCI) cruises. Alaska Fish. Sci. Center, NOAA, Seattle, WA, 119 p.

[5] J. Runge. 1990. Insti. Maurice Lamontagne, Mont-Joli, Quebec, Canada, pers. commun. 1990.

[6] J. Runge. 1993. Inst. Maurice Lamontagne, Mont-Joli, Quebec, Canada, unpubl. data.

[7] Jeffry Napp, Nat. Mar. Fish. Serv., Alaska Fishereis Science Center, Seattle, WA, pers. commun. 1993.

[8] Kenric Osgood, Dep. Oceanography, Univ. Washington, Seattle, WA, pers. commun. 1993.

pared to <20 µg-at L^{-1} in the other years); in surface waters they were lowest in 1987 (mostly <2 µg-at L^{-1}), followed by 1986 (<4 µg-at L^{-1}) and 1989 (<5 µg-at L^{-1}) (Fig. 2). Surface nitrate distributions generally reflected density structure. Isopleths of density (Fig. 2), salinity, and temperature show larger

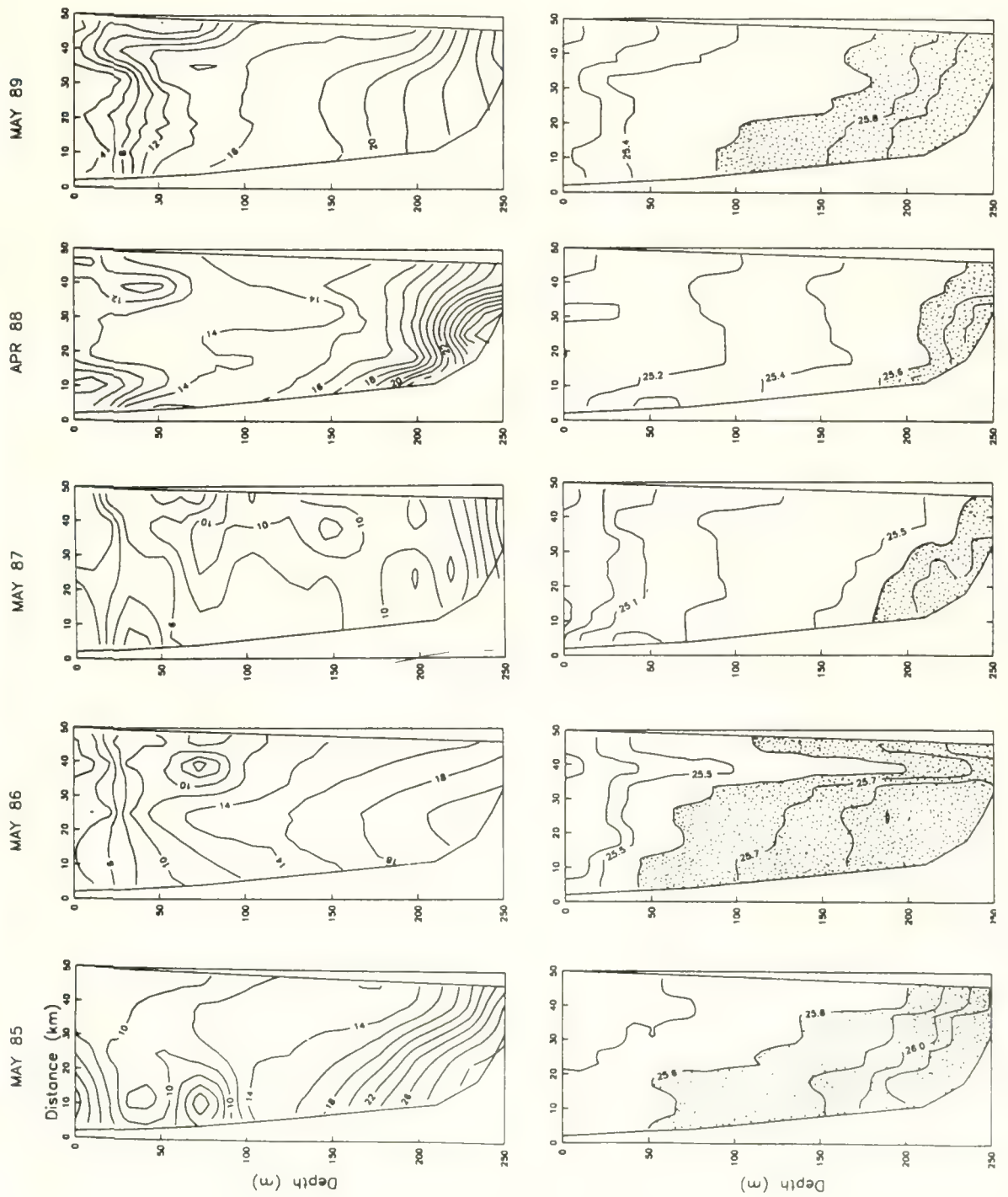

Figure 2

Profiles of nitrate (upper panel, µg-at L^{-1}) and density (lower panel, σ_t) across Shelikof Strait during spring, 1985–89. Water denser than σ_t=25.6 is shaded. The transect is viewed looking westward; distances are given from the Kodiak Island shore. Sampling dates are given in Table 2.

volumes of high density (high salinity) bottom water in 1985, 1986, and 1989 compared with other years. The upper mixed layer generally was deepest on the northern end of the transect, near the Alaska Peninsula, with a steeply sloping density gradient near the middle. The exception, in 1988, is discussed later. Averaged across the Strait, the upper mixed layer was deepest in 1985 and shallowest in 1986 and 1987.

Observations of phytoplankton clogging sampling nets during the cruises showed that the spring bloom of large diatoms occurred latest in 1985. By this approximation, what probably was the major spring bloom in the Strait began after the first week of May in 1985, whereas it already was well underway when we began sampling in early May 1986 and 1989 and late April 1988. A grid of sampling stations that extended to the northern end of the Strait in 1985 showed that the bloom in that year formed first in a band along the middle of the Strait for virtually its full length of 300 km. Our grid interval was not sufficiently fine to resolve the width of the bloom feature, but our findings are consistent with a diameter <25 km.

Our samples were dominated numerically by copepod nauplii, which composed from 46 to 82% of all organisms sampled along the transect over the five-year period (Table 1), followed in most years by copepods eggs, from 3.5 to 35%. Of the remaining taxonomic categories, only a few ever contributed more than 5% of the total organism count: small copepods (including copepodid stages), tintinnids, rotifers, and polychaete larvae. None of these ever exceeded 15% of the total count.

The integrated (0–60 m depth) abundance of microzooplankton at the primary sampling stations increased across the Strait from south to north (see Fig. 3 for copepod nauplii). Average abundances of nauplii, eggs, and all other organisms were highest in 1986 and 1987. For copepod nauplii, abundance was lowest in 1985 and intermediate in 1988 and 1989 (Table 1). In 1985, near-surface concentrations averaged 86% of those at 10-m depth. Therefore, the assumption of uniform concentration of organisms in the upper 10 m may have introduced a small upward bias in the integrations from 1986 onward.

The 7-km resolution of microzooplankton obtained across the Strait in 1988 (Fig. 4) shows a more complex pattern of distribution than suggested by other transects. Specifically, comparatively large numbers of nauplii and other microzooplankton were found at stations 56 and 57, nearly equivalent to populations at the two northern stations. Both groups of stations were marked by waters of lower surface nitrate concentration (Fig. 2) associated with flow around a dynamic high in the middle of the Strait (Fig. 5). The two groups of stations differed from each other in the composition of planktonic eggs (greater concentrations at stations 60, 61) and other microzooplankton (greater at 56 and 57) and in temperature and salinity. The southern "limb" of the anticylconic feature was about 0.1° C warmer and 0.05 g kg^{-1} more saline than the northern limb. Chlorophyll data show high chlorophyll-*a* concentrations (up to 6 µg L^{-1}) and high integrated chlorophyll-*a* (140–180 mg m^{-2}, 0–100 m) in the two limbs of the ACC surrounding the anticyclonic feature; the lowest chlorophyll-*a* (10 mg m^{-2}) was found in the middle.

Copepod nauplii were found mostly in the upper 30 m, though they extended deeper at some stations in 1985 and 1988 (Fig. 6). Naupliar concentrations were greater in the northern half of the transect in 1985, 1986, and 1987; they were distinctly bipolar in 1988; and in 1989 maximum concentrations of both nauplii (Fig. 6) and chlorophyll-*a* (Fig. 7) occurred in the center of the Strait. Maximum naupliar concentrations encountered at any depth across the Strait per transect ranged from 18 L^{-1} in 1985 to 144 L^{-1} in 1987, both at 20 m depth at station 60. Planktonic copepod eggs also occurred mostly in the upper 30 m but exhibited a variety of across-shelf patterns that were

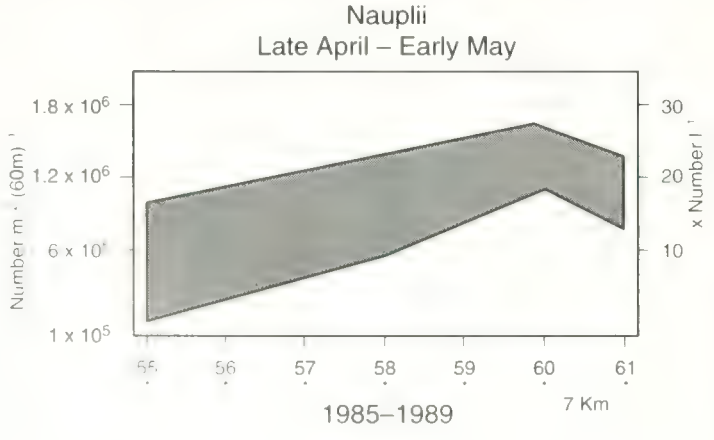

Figure 3

Across-strait patterns of integrated abundance (No. m^{-2}) and average concentration (no. L^{-1}) of copepod nauplii from surface to 60–m depth during spring at the primary time-series stations, marked with asterisks. Upper and lower lines describe the maximum and minimum values observed, 1985–89.

not always the same as those found for nauplii. Maximum egg concentrations ranged from 2.2 L^{-1} in 1988 (at 30 m depth) to 45 L^{-1} in 1986 (10 m depth), both at station 59. Most eggs and nauplii were in the upper mixed layer. Since sampling in 1987 occurred in late May, the relatively high abundance of nauplii may be attributed to time of year. Consequently, a statistical comparison between transects focussed on the other four years, which were sampled the last week of April and first week of May. This time period is close to the time of peak larval hatching. Abundance was statistically different among transects (Quade test $0.025 < P < 0.05$). The lowest (1985) and highest (1986) concentrations were significantly different at $\alpha = 0.05$; the intermediate concentrations of 1988 and 1989 differed from those in 1985 (but not 1986) at $\alpha = 0.10$ (Multiple comparisons of ranks).

The lengths of sampled nauplii showed positively skewed frequency distributions with peak abundance between 100 and 150 µm TL in all years and nearly identical cumulative distribution functions (Fig. 8). Median size differed by less than 15 µm among years and averaged 140 µm during the five–year period. The average length: width ratio of nauplii measured in this study was 2.2, with a standard deviation of 0.1 (n=1500). Consequently, our mesh, 41 µm on a side and 58 µm on the diagonal, should have retained some nauplii >90 µm long and all nauplii >128 µm. Our data showed a steep decline in frequency of nauplii with length <110 µm, between the above estimates, and width <50 µm, corresponding to the relationship 110/2.2 = 50. Most of the nauplii did not have urosomal segments, so total length and maximum width are equivalent to prosome length and width for most of our data.

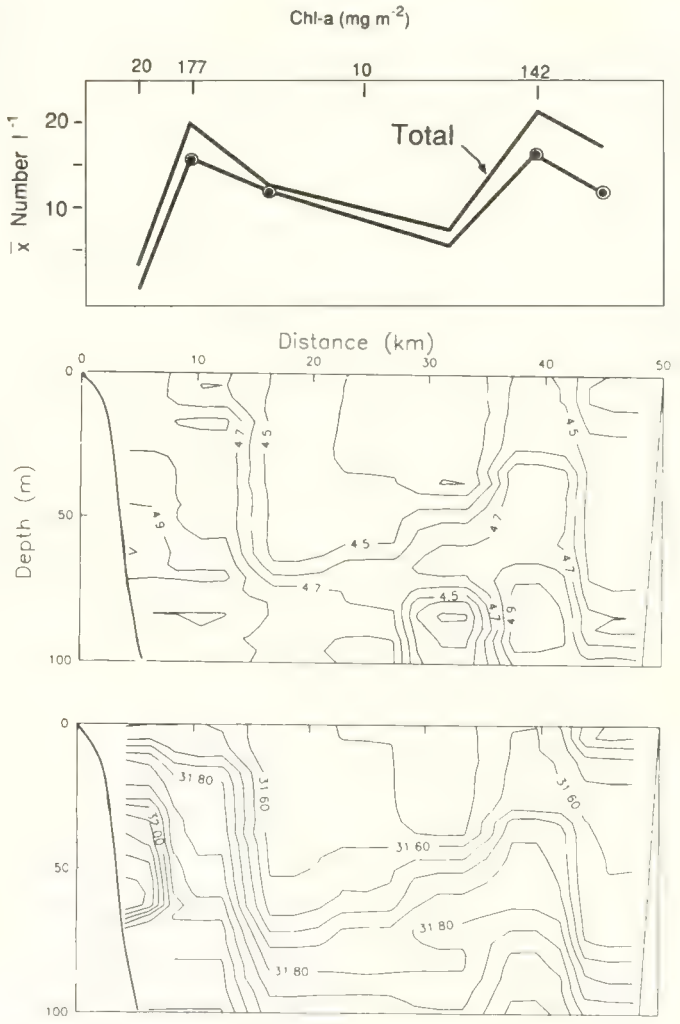

Figure 4

Mean number of nauplii and total microzooplankton per liter in the upper 60 m across the study transect in April 1988 (top panel), viewed looking westward. Numbers at the top of the panel show integrated (0–100 m) chlorophyll-a concentrations (mg m^{-2}). Temperature (°C) and salinity (g kg^{-1}) are shown in the middle and bottom panels, respectively. Data can be compared with nutrient distributions (Fig. 2), dynamic topography (Fig. 5), and depth distributions of nauplii (Fig. 6).

The abundance and size distribution of eggs differed substantially between years (Fig. 8). The greatest number (and smallest median size [ca. 75–µm diameter]) of planktonic eggs was present in 1986; the fewest eggs occurred in 1988, when median size was the largest (ca. 165 µm).

Abundances of potentially significant contributors to the standing stocks of copepod eggs and nauplii are given in Table 2. Among the taxa of interest, *Calanus pacificus* had low adult female numbers because most individuals were in copepodid stage 5 (C5) during spring. Other adult female copepods were broadly distributed across the Strait, but the maximum concentration of each taxon occurred in the northern half (among stations 58–61) in all but one instance. The across-Strait patterns of low and high abundances within species were similar from year to year and statistically significant (Spearman rank correlation test, P<0.05). The shift in mesh sizes for *Pseudocalanus* spp. collections limits the between-transect comparisons that can be made. (Note that there are interspecific differences within

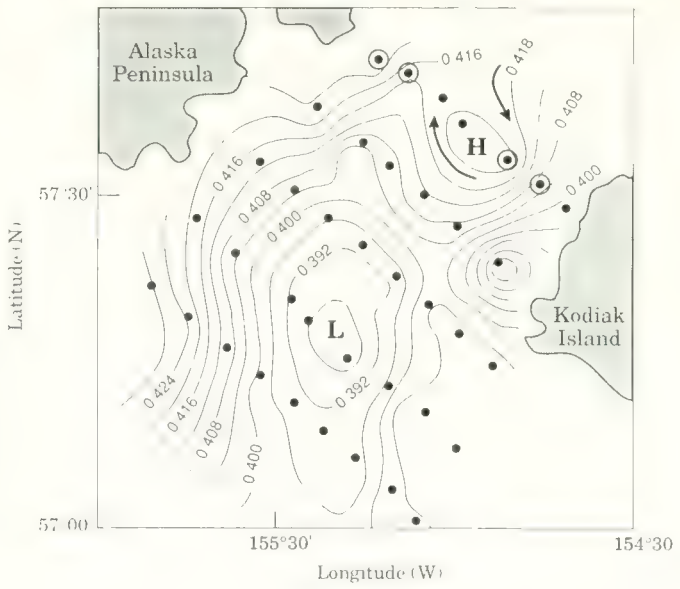

Figure 5

Contours of 0–150 m dynamic height in western Shelikof Strait during April 1988. Solid circles show locations of CTD stations. The study transect is the farthest northeast section. Open circles denote those transect stations with the highest microzooplankton standing stocks (cf. Figs. 4, 6). A dynamic high (H) and low (L) are labelled; arrows show inferred flow.

the genus that prohibit any simple correction for different mesh collections: see Frost, 1987.) Within these limitations, data for 1985 and 1986 (333 µm) were statistically different (Wilcoxon signed rank test, P=0.076), whereas the multi-year comparison for early spring samplings (1986, 1988, 1989: 150 µm mesh) showed no statistically significant differences (Quade test, α= 0.05). Among early spring values, there were no statistically significant differences in abundance of *Metridia* spp..

Discussion

The method of sampling and preservation used in this study under-represented smaller components of the microzooplankton (James, 1991) but was adequate to capture the majority of prey items of larval walleye pollock based on prey sizes reported from earlier studies of Clarke (1984: Bering Sea), Nishiyama and Hirano (1983, 1985: Bering Sea), Dagg et al. (1984: Bering Sea); and Kendall et al. (1987: Shelikof Strait). For small larvae of 5–10 mm standard length (SL) in those studies, copepod nauplii composed the majority of items found in larval stomachs. They also made up the bulk of estimated volume or carbon content of prey when these values were calculated (Incze et al., 1984; Nishiyama and Hirano, 1983). The 10–m vertical resolution of our sampling method almost certainly failed to detect the highest concentrations of prey available to larval walleye pollock under some conditions, such as in small patches (Owen, 1989), but probably reflects adequately the average abundances found at different depths in the water column, in different sections across the Strait and in different transects.

Size-frequency distributions of sampled nauplii and dimensions of the sampling mesh suggest that there was virtually complete retention of nauplii with total length ≥ 125 µm. In most cases these measurements were carapace ("prosome") lengths. Unpublished data from stomach content studies (Canino, 1992[9]) show that ca. 98% of the nauplii consumed by larval walleye pollock collected during our cruise in May 1989 had carapace length ≥ 125 µm. Between 60 and 70% of the nauplii in our samples were of this size (Fig. 8).

Concentrations and integrated abundances of nauplii differed across Shelikof Strait in patterns that appear to be related to circulation features. Our data indicated that standing stocks and maximum concentrations of copepod nauplii in spring were greatest in the ACC, which is also where greatest chlorophyll-*a* concentrations occurred (latter data for 1988, 1989; cf. Figs. 4, 6, 7). The lowest naupliar concentrations of the early spring samplings occurred in 1985, which had the weakest stratification. In general, nauplii were most abundant at 20-m depth except in 1988, when maximum concentrations occurred at 30-m depth in the deeper mixed perimeter of the anticyclonic feature. The lowest standing stock of nauplii coincided with the latest apparent phytoplankton bloom in 1985, but we cannot determine if lower individual copepod egg production rates or lower standing stocks of copepods were responsible because we lack adequate collections (150–µm mesh) of *Pseudocalanus* spp. in 1985. Alternatively, the low naupliar standing stocks could have been due to higher predation, but our data show that springtime populations of predators were generally low and were similar among years.

Our data suggest that the distribution of copepod nauplii and some other microzooplankton across

[9] M. Canino. 1992. Natl. Mar. Fish. Serv., Alaska Fisheries Science Center, Seattle, WA, unpubl. data.

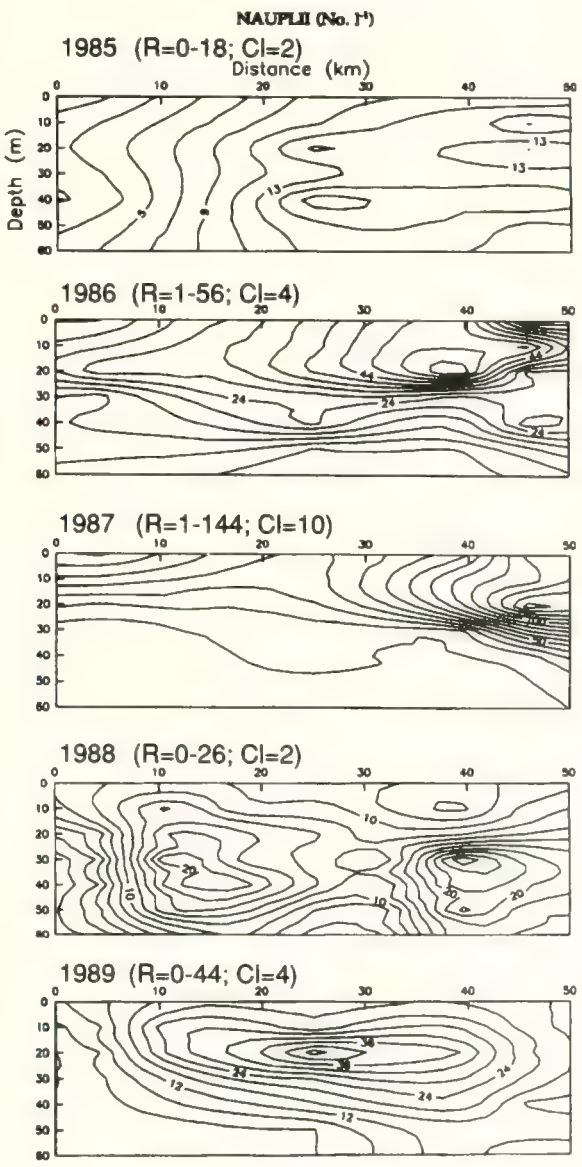

Figure 6

Contour plots of naupliar concentrations (no. L^{-1}) across Shelikof Strait during spring. Numbers in parentheses after the year (upper left of each plot) show the range (R) of data and the contour interval (CI) used in plotting. Transects are viewed looking westward.

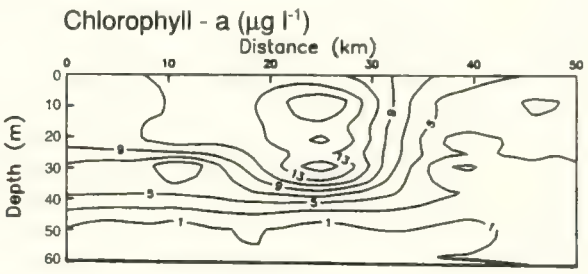

Figure 7

Chlorophyll-*a* distributions across Shelikof Strait, May 1989, looking westward (data may be compared with nutrient and hydrographic structure in Fig. 2 and naupliar concentrations in Fig. 6).

Shelikof Strait were subject to the influence of baroclinic instabilities. The timing and rotational sense of these instabilities therefore may have a large influence not only on the distribution of walleye pollock larvae themselves (Reed et al., 1989; Incze et al., 1990; Vastano et al., 1992), but also on the feeding conditions they experience. For example, the feature sampled in 1988 covered a substantial portion of the main spawning and hatching area. Although we do not have extended observations of this feature, Vastano et al. (1992) showed that eddy-like features may remain near the hatching area for as long as two weeks, a substantial portion of the hatching period (Yoklavitch and Bailey, 1990). If walleye pollock larvae migrate vertically into the center of a dynamic high after hatching, then the amount of time that passes before they are advected into better feeding conditions (in this case at the periphery of the high) may be important to early larval feeding and growth.

The average integrated abundance of copepod nauplii across the Strait was different for the various transects. The maximum values that were seen in 1987 probably can be attributed to the comparatively late sampling of that year. However, among the four years with similar timing of transect sampling, there remained statistically significant differences that may have been important to hatching walleye pollock larvae (see Canino et al., 1991, for feeding conditions and larval RNA/DNA ratios). Since hatching takes place over a relatively short time period (Yoklavitch and Bailey, 1990), the phasing of hatching and upper layer conditions may play an important role in establishing the larval year class. Unfortunately, we do not know how long the observed conditions persisted in each year relative to the population hatching time or to other requirements of the early feeding period in larval development. Advection (Incze et al., 1989) and short-term fluctuations in mesoscale circulation (Vastano et al., 1992) may cause conditions in the Strait to change quickly, requiring more frequent sampling and improved techniques to rapidly assess prey distributions.

Nauplii that were most abundant in the diet of larval pollock must have come from copepods large enough to be retained by mesh sizes used on the

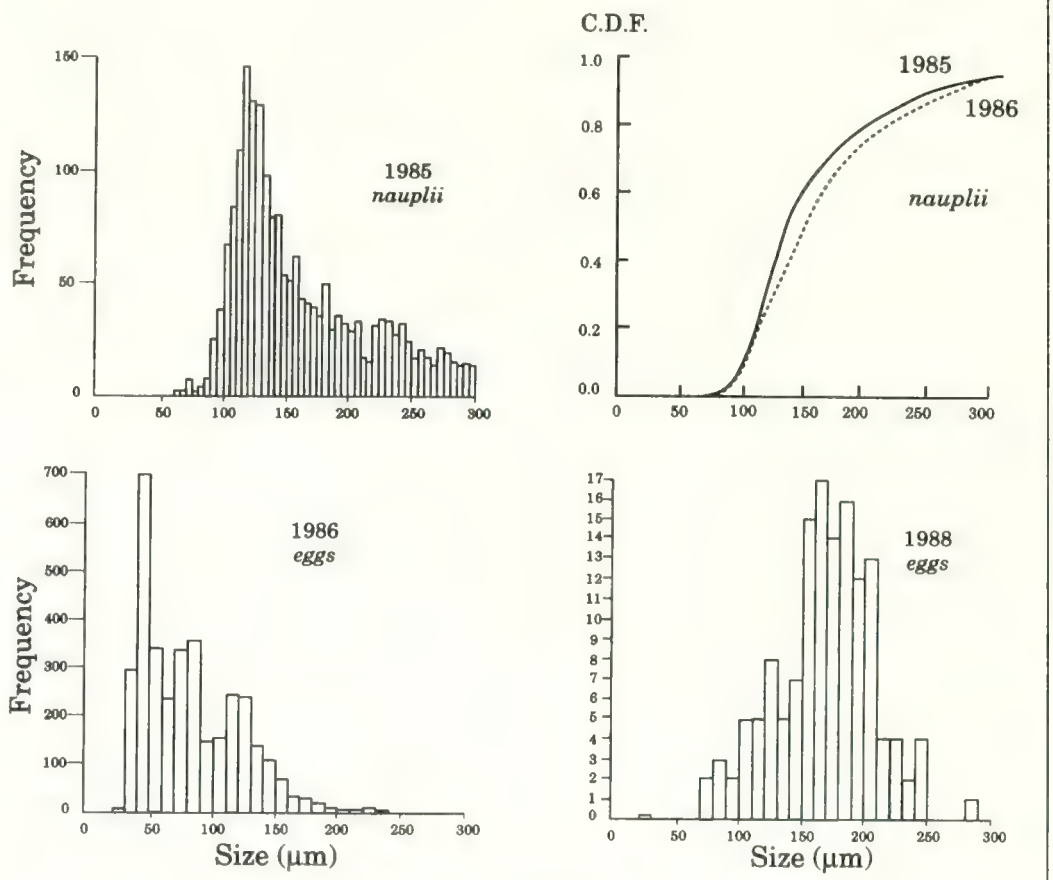

Figure 8

Size-frequency distribution of nauplii and eggs. Graph in upper left shows size frequency of nauplii from 1985. Graph in upper right shows the full range of size distributions of nauplii by comparing the cumulative distribution functions (CDF) for the two extremes, 1985 and 1986. Size distributions of eggs are shown in the two lower graphs for years with the smallest (1986) and largest (1988) eggs. Note changes in frequencies shown on the various ordinates.

bongo samplers (Table 2). Based on the average abundance and fecundity (see Methods) of adult female copepods, the approximate contribution of each species to the daily production of NI would be: *Pseudocalanus* spp., >75%; *Metridia pacifica*, 18%; *Calanus marshallae*, 4%; and *Calanus pacificus*, <1%. These percentages are useful only for the relative scaling they permit; many factors may influence copepod reproduction rates, and rates of development and mortality will influence further the total standing stock of nauplii contributed by each species. These results agree with those of Dagg et al. (1984) with respect to the importance of *Pseudocalanus* spp. naupliar production for larval walleye pollock feeding. Our results differ in the greater inferred role of *Metridia* spp., probably because of the deep waters of the Shelikof sea valley compared with the Bering Sea shelf where Dagg and his coauthors worked. The numerous small nauplii <120 µm that we sampled are from unknown sources. The abundance and fecundity of *M. pacifica* suggest that they were significant contributors to populations of planktonic eggs and that *Calanus marshallae* plays a lesser role. A large number of small planktonic eggs <150–µm diameter are not accounted for by the adult female copepods retained by our nets.

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Table 2

Abundance (no. m^{-2}) of adult female copepods on a transect across western Shelikof Strait during spring. Data are listed vertically showing mean, (standard deviation) and range. *Metridia pacifica* is *Metridia pacifica* / *M. lucens*; unidentified *Metridia* spp. are not included in this tally. Hyphens indicate absence of data.

	Year and day				
Taxon and mesh size	1985 (3 May)	1986 (3 May)	1987 (19 May)	1988 (27 Apr)	1989 (10 May)
Pseudocalanus spp.	—	14,183	41,058	13,634	8,450
150 μm		(6,523)	(25,527)	(4,128)	(4,026)
		6,758–18,994	6,108–78,976	7,846–20,316	2,870–12,563
Pseudocalanus spp.	9,119	16,232	33,098	—	—
333 μm	(4,767)	(8,295)	(19,398)		
	2,509–16,110	7,848–30,573	6,273–51,729		
Calanus marshallae	130	82	610	125	618*
333 μm	(146)	(72)	(532)	(93)	(786)
	0–431	0–211	0–1,343	0–238	0–2,196
Metridia pacifica	5,082	3,168	9,537	3,211	2,713
333 μm	(4,128)	(1,956)	(5,570)	(1,626)	(2,549)
	68–11,899	24–6,340	288–5,715	288–5,715	0–6,945
Calanus pacificus	15	2	0	28	133
333 μm	(27)	(4)		(61)	(228)
	0–73	0–9		0–164	0–521

McCauley for early work with microzooplankton sorting, D. Siefert for processing net zooplankton samples and our many sea-going colleagues for their help in the field. Our work benefitted from discussions with A. Kendall, K. Bailey, J. Schumacher, and J. Runge, and our manuscript from comments by M. Mullin, J. Napp, and an anonymous reviewer.

Literature cited

Bailey, K. M., and E. D. Houde.
1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. 25:1–83.

Batchelder, H. P., and C. B. Miller.
1989. Life history and population dynamics of *Metridia pacifica*: results from simulation modelling. Ecol. Modelling 48:113–136.

Buckley, L. J., and R. G. Lough.
1987. Recent growth, biochemical composition and prey field of larval haddock (*Melanogrammus aegelfinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can. J. Fish. Aquat. Sci. 44:14–25.

Buckley, L. J., A. S. Smigielski, T. A. Halavik, and G. C. Laurence.
1990. Effects of water temperature on size and biochemical composition of winter flounder *Pseudopleuronectes americanus* at hatching and feeding initiation. Fish. Bull. 88:419–428.

Canino, M. F., K. M. Bailey, and L. S. Incze.
1991. Temporal and geographic differences in feeding and nutritional condition of larval walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska. Mar. Ecol. Progr. Ser. 79:27–35.

Clarke, M.
1984. Feeding behavior of larval walleye pollock, *Theragra chalcogramma* (Pallas), and food availability to larval pollock in the southeastern Bering Sea. Ph.D. thesis, Univ. California, San Diego, 208 p.

Conover, W. J.
1971. Practical Non-Parametric Statistics. John Wiley & Sons, New York, 493 p.

Cushing, D. H.
1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26:249–293.

Dagg, M. J., M. E. Clarke, T. Nishiyama, and S. L. Smith.
1984. Production and standing stock of copepod nauplii, food items for larvae of the walleye pollock *Theragra chalcogramma* in the southeastern Be ring Sea. Mar. Ecol. Prog. Ser. 19:7–16.

Davis, C. S., G. R. Flierl, P. H. Wiebe, and P. J. S. Franks.
1991. Micropatchiness, turbulence and recruitment in plankton. J. Mar. Res. 49:109–151.

Frost, B. W.
1987. A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. Can. J. Zool. 67:525–551.

Fulton, J. D.
1972. Keys and references to the marine Copepoda of British Columbia. Fish. Res. Board Can. Tech. Rpt. 313, 63 p.

Gamble, J. C., and L. A. Fuiman.
1987. Evaluation of *in situ* enclosures during a study of the importance of starvation to the vulnerability of herring larvae to a piscine predator. J. Exp. Mar. Bol. Ecol. 113:91–103.

Houde, E. D.
1987. Fish early life history dynamics and recruitment variability. Am. Fish. Soc. Symp. 2:17–29.

Incze, L. S., M. E. Clarke, J. J. Goering, T. Nishiyama and A. J. Paul.
1984. Eggs and larvae of walleye pollock and relationships to the planktonic environment. *In* Proc. workshop on walleye pollock and its ecosystem in the eastern Bering Sea, p. 109–159. NOAA Tech. Mem. NMFS F/NWC-62.

Incze, L. S., A. W. Kendall Jr., J. D. Schumacher, and R. K. Reed.
1989. Interactions of a mesoscale patch of larval fish (*Theragra chalcogramma*) with the Alaska Coastal Current. Cont. Shelf Res. 9:269–284.

Incze, L. S., P. B. Ortner, and J. D. Schumacher.
1990. Microzooplankton, vertical mixing and advection in a larval fish patch. J. Plankton Res. 12:365–379.

James, M. R.
1991. Sampling and preservation methods for the quantitative enumeration of microzooplankton. N.Z. J. Mar. Freshwater Res. 25:305–310.

Kendall Jr, A. W., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert.
1987. Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull. 85:499–521.

Lasker, R.
1981. The role of a stable ocean in larval fish survival and subsequent recruitment. *In* R. Lasker, (ed.) Marine fish larvae: morphology, ecology and relation to fisheries, p. 80–87. Washington Sea Grant Program, Seattle.

McKenzie, B. R., W. C. Leggett, and R. H. Peters.
1990. Estimating larval fish ingestion rates: Can laboratory derived values be reliably extrapolated to the wild? Mar. Ecol. Progr. Ser. 67:209–225.

Moller, H.
1984. Reduction of a larval herring population by jellyfish predator. Science 224:621–622.

Mysak, L. A., R. D. Muench, and J. D. Schumacher.
1981. Baroclinic instability in a downstream varying channel: Shelikof Strait, Alaska. J. Phys. Oceanogr. 11:950–969.

Nishiyama, T., and K. Hirano.
1983. Estimation of zooplankton weight in gut of larval walleye pollock (*Theragra chalcogramma*). Bull. Plankton Soc. Japan 30:159–170.
1985. Prey size and weight relations in larval walleye pollcok (*Theragra chalcogramma*). Bull. Plankton Soc. Japan 32:45–59.

Owen, R. W.
1989. Microscale patchiness in the larval anchovy environment. Rapp. P.-v. Reun. Cons. int. Explor. Mer. 178: 364–368.

Paul, A. J., K. O. Coyle, and D. A. Ziemann.
1990. Variations in egg production rates by *Pseudocalanus* spp. in a subarctic Alaska Bay during the onset of feeding by larval fish. J. Crust. Biol. 10:648–658.

Phinney, D. A., and C. S. Yentsch.
1985. A novel phytoplankton chlorophyll technique: Toward automated analysis. J. Plankton Res. 7:633–642.

Purcell, J. E., and J. J. Grover.
1990. Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia. Mar. Ecol. Progr. Ser. 59:55–61.

Reed, R. K., and J. D. Schumacher.
1989. Transport and physical properties in central Shelikof Strait, Alaska. Cont. Shelf Res. 9:261–268.

Reed, R. K., J. D. Schumacher and L. S. Incze.
1987. Circulation in Shelikof Strait, Alaska. Phys. Oceanogr. 17:1546–1554.

Reed, R. K., L. S. Incze, and J. D. Schumacher.
1989. Estimation of the effects of flow on dispersion of larval pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska. Can. Spec. Publ. Fish. Aquat. Sci. 108:239–246.

Rothschild, B. J., and T. R. Osborne.
1988. Small-scale turbulence and plankton contact rates. J. Plankton Res. 10:465–474.

Runge, J. A.
1984. Egg production of the marine, planktonic copepod, *Calanus pacificus* Brodsky: laboratory observations. J. Exp. Mar. Biol. Ecol. 74:53–66.

Schumacher, J. D., and A. W. Kendall Jr.
1991. Some interactions between early life stages of walleye pollock and their environment in the western Gulf of Alaska. CalCOFI Rep. 32:22–40.

Theilacker, G. H., and Y. Watanabe.
1989. Midgut cell height defines nutritional status of laboratory raised larval northern anchovy, *Engraulis mordax*. Fish. Bull. 87:457–469.

Vastano, A. C., L. S. Incze, and J. D. Schumacher.
1992. Observation and analysis of fishery processes: larval pollock at Shelikof Strait, Alaska. Fish. Oceanogr. 1:20–31.

Yentsch, C. S., and D. W. Menzel.
1963. A method for the determination of phytoplankton chlorophyll and phaeophytin-*a* fluorescence. Deep Sea Res. 10:221–231.

Yoklavich, M. M., and K. Bailey.
1990. Hatching period, growth and survival of young walleye pollock (*Theragra chalcogramma*) as determined from otolith analysis. Mar. Ecol. Progr. Ser. 64: 13–23.

Marine distribution and size of juvenile Pacific salmon in Southeast Alaska and northern British Columbia

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Abstract.—Distribution and size during their first summer at sea were determined for juvenile salmon (*Oncorhynchus* spp.) caught in oceanic waters off northern British Columbia and Southeast Alaska, and in marine waters within the Alexander Archipelago of Southeast Alaska. More than 10,000 juvenile salmon were caught in 252 purse-seine sets during August 1983, July 1984, and August 1984. Distribution was patchy; juvenile salmon were highly aggregated, rather than dispersed randomly. Distribution and size of pink salmon (*O. gorbuscha*), sockeye salmon (*O. nerka*), and chum salmon (*O. keta*) were similar but differed from coho salmon (*O. kisutch*). Chinook salmon (*O. tshawytscha*) were excluded from most analyses because few were caught. Sizes were consistent with the concept that juvenile salmon in more northern and seaward locations had been at sea longer than those in more southern and inshore locations. Juvenile salmon migration up the Pacific coast did not peak in abundance off Southeast Alaska until August; movement from inside to outside waters was not complete by the end of August. The migration band of juvenile salmon in outside waters of Southeast Alaska extended beyond the continental shelf to at least 74 km offshore, twice the distance previously reported.

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The general migratory movements of Pacific salmon (*Oncorhynchus* spp.) during their first year at sea have been described (Hartt and Dell, 1986), but little information is available on the seaward migration of juvenile salmon from the inside waters of Southeast Alaska into the Gulf of Alaska. Salmon moving seaward from streams inside Southeast Alaska pass first through the complex waterways of the Alexander Archipelago, the "inside waters" of Southeast Alaska. Upon entering the Gulf, these salmon either occupy outer coast inlets or move into exposed outside waters. Salmon entering exposed outside waters either migrate north along the coast or move progressively farther offshore (Hartt and Dell, 1986). Determining when and at what size juvenile salmon from Southeast Alaska utilize different habitats during their seaward migration to the Gulf may facilitate understanding the high mortality during their first few months at sea (Parker, 1968; Bax, 1983; Furnell and Brett, 1986).

Our goal was to ascertain the distribution and migration of juvenile Pacific salmon during their first summer at sea after they leave nearshore estuarine habitats. Specific objectives were 1) to determine relative distribution, abundance, and size of juvenile salmon in exposed outside waters, in protected waters adjacent to the outer coast, and in the inside waters of Southeast Alaska, and 2) to compare abundance and size of juvenile salmon in outside waters of Southeast Alaska and northern British Columbia.

Methods

Study area and time

The study area extended from Lituya Bay, Southeast Alaska, to the northern end of Vancouver Island, British Columbia (Fig. 1). Three major habitats were sampled: 1) outside waters (the North Pacific Ocean and Gulf of Alaska adjacent to the outer coast of Southeast Alaska and British Columbia); 2) outer coast inlets (protected waters along the outer coast of Southeast Alaska); and 3) inside waters (marine waters within the Alexander Archipelago). Southeast Alaska was further divided at lat. 56°N into a northern and southern region for some analyses. Fishing effort was concentrated in the northern region of Southeast Alaska (Fig. 1).

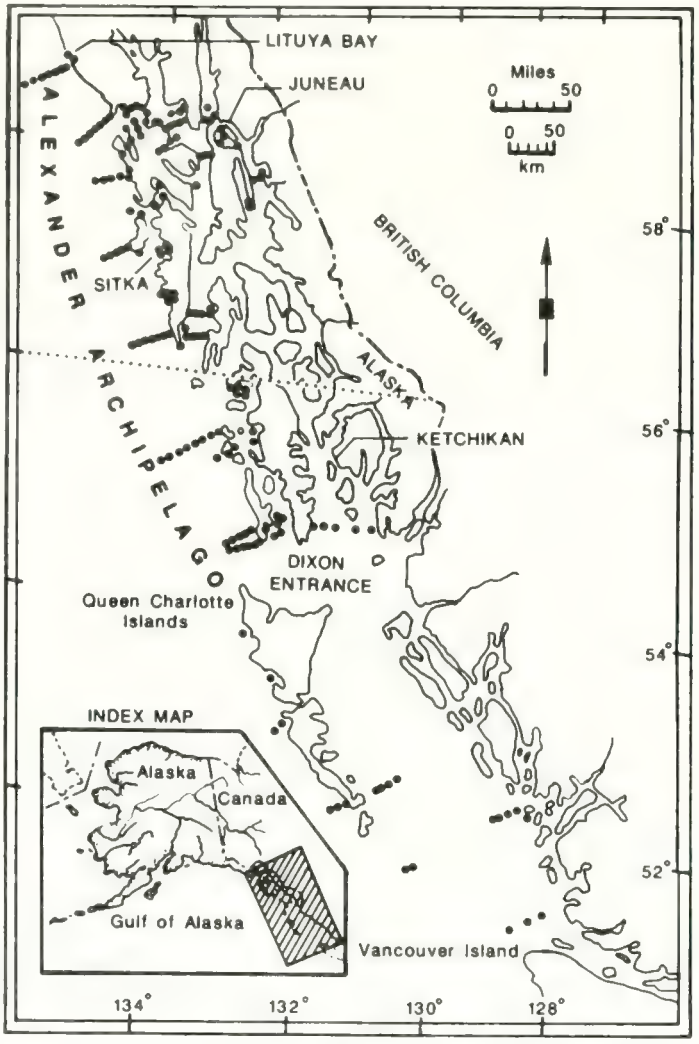

Figure 1

Locations seined in Southeast Alaska and British Columbia in 1983 and 1984. The delineation between northern and southern Southeast Alaska is indicated by the dotted line (running along 56°N lat.).

We sampled in Southeast Alaska during three periods: 6 August–3 September 1983 (hereafter designated August 1983), 9–24 July 1984, and 1–30 August 1984. Sampling in British Columbia was conducted 1–6 July 1984.

Survey stations in outside waters were located along transects perpendicular to shore (Fig. 1). The nearshore station of each transect was as close to land as net depth and safety permitted. Stations were usually sampled progressively offshore at 5.6 km (3 nautical miles [nmi]) intervals in 1983 and at 9.3 km (5 nmi) intervals in 1984. Sampling generally did not extend beyond 37 km offshore except in Southeast Alaska in August 1984, when transects extended as far as 74 km offshore. Distances are rounded to the nearest 1 km in the text.

In large passages in the inside waters, sets were often made along transects near the entrance to outside waters (Fig. 1). Multiple sets were also made in clusters in the larger inlets.

Gear

Stations were sampled with table and drum seines as described by Browning (1980). The 28-m NOAA RV *John N. Cobb* fished a table seine in August 1983 and August 1984; the 24-m FV *Bering Sea* fished a drum seine in July 1984. Sets were made at predetermined locations without reference to visual or instrument sightings of fish. All sets were round hauls: the net was set in a semi-circle, held open 3–5 minutes, closed, pursed, and retrieved by means of a hydraulic power block (table seine) or a hydraulic roller (drum seine). Only catches from effective seine sets are listed (Table 1).

Although the seines differed in size, mesh, and area enclosed, the two nets were assumed to be comparable in their ability to capture juvenile salmon. The table seine was 455 m long; depth tapered from 37 m in the wing to 11 m in the bunt; web sizes (stretch mesh) were 89 mm and 57 mm in the wing, and 25 mm in the bunt. The drum seine was 503 m long, 46 m deep, and had 32–mm mesh in the wing, and 25 mm in the bunt. Depths fished were assumed to be adequate for sampling juvenile pink (*O. gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), and coho (*O. kisutch*) salmon, which usually occupy the upper 10 m of the water (Manzer, 1964; Godfrey et al., 1975; Hartt, 1975). To compensate for the larger surface area enclosed by the drum seine (20,150 m^2) compared to the table seine (16,467 m^2), drum seine catches (July 1984) were reduced during analyses by 18.3% to standardize the catch per unit of effort (CPUE). This standardization caused the July 1984 catches reported to be sometimes less than the number of fish measured for size that period.

Catch processing and analysis

The catch was processed aboard ship and in the Auke Bay Laboratory. The number of juvenile salmon captured in each set was counted if the catch was small (i.e., <100 fish) or estimated gravimetrically if the catch was large. Up to 100 salmon from each set were preserved in 10% formalin in seawater

Table 1

Number of juvenile salmonids caught by species, period, and habitat. All seining occurred in Southeast Alaska (SE AK) except in July 1984 when the outside waters of British Columbia (B.C.) were also sampled.

Period	Habitat	Number of sets	Number of fish caught					
			Pink[1]	Chum[2]	Sockeye[3]	Coho[4]	Chinook[5]	All species
August 1983	Inside waters	54	2,011	385	178	201	3	2,778
	Outer coast inlet	27	680	85	0	23	1	789
	Outside waters	8	20	2	9	27	0	58
	Subtotal	89	2,711	472	187	251	4	3,625
July 1984	Inside waters	18	91	16	17	197	19	340
	Outer coast inlet	14	10	2	0	24	0	36
	Outside waters							
	B.C.	21	573	189	581	33	5	1,381
	SE AK	33	181	34	109	28	1	353
	Subtotal	86	855	241	707	282	25	2,110
August 1984	Inside waters	37	1,850	163	23	375	23	2,434
	Outer coast inlet	4	0	12	0	3	0	15
	Outside waters							
	≤37 km seaward	26	866	152	171	128	5	1,322
	>37 km seaward	10	522	63	119	26	0	730
	Subtotal	77	3,238	390	313	532	28	4,501
All	Inside waters	109	3,952	564	218	773	45	5,552
	Outer coast inlet	45	690	99	0	50	1	840
	Outside waters	98	2,162	440	989	242	11	3,844
	Total	252	6,804	1,103	1,207	1,065	57	10,236

[1] *Oncorhynchus gorbuscha*
[2] *O. keta.*
[3] *O nerka*
[4] *O kisutch*
[5] *O. tshawytscha*

for later species identification and size measurements (fork length [FL] to nearest mm). If more than 100 juvenile salmon were captured in a set, the excess fish were released alive.

Graphs (Chambers et al., 1983) and exploratory data analysis (Tukey, 1977) were used to present catch data because the data had a nonnormal distribution with values clumped at zero (many seine sets did not capture juvenile salmon). Transformations of catch data were ineffective in making the distribution more symmetrical. Quantile plots (Chambers et al., 1983), which show individual catches from smallest to largest, were used to describe the statistical distribution of catches of each species. Chinook salmon (*O. tshawytscha*) were excluded from the remaining analyses because few were caught. Morisita's Index of Aggregation (Morisita, 1959; Poole, 1974) was used to test whether each salmon species was randomly dispersed or aggregated in marine waters of Southeast Alaska.

Morisita's index is defined as

$$I_\delta = \frac{\sum_{i=1}^{N} n_i (n_i - 1)}{n(n-1)} N,$$

where N is the number of samples, n_i is the number of individuals in the ith sample, and n is the total number of individuals in all samples. The significance of I_δ is tested with the F test described by Poole (1974). Spearman's rho (ρ) correlation test (Daniel, 1978) was used to measure association between each possible pairing of the four main species caught (pink, chum, sockeye, and coho salmon).

For comparisons, catch data were split into cells by 1) species, 2) habitat (outside waters, outer coast inlets, and inside waters), 3) region (northern Southeast Alaska, southern Southeast Alaska, and British Columbia), and 4) time period (August 1983, July 1984, and August 1984). CPUE was used as an index of abundance; frequency of occurrence (FO)

was used as a measure of presence of juvenile salmon.

Five null hypotheses were tested during fish length analyses of the four species. The first four hypotheses stated that size of a species did not differ for fish from 1) outside and inside waters, 2) outside waters >37 km offshore and ≤37 km offshore, 3) northern and southern waters, and 4) July and August of 1984. The alternate hypotheses stated that fish were larger in 1) outside than inside waters, 2) outside waters >37 km offshore than outside waters ≤37 km offshore, 3) northern than southern waters, and 4) August than July of 1984. The fifth hypothesis stated that length did not differ among species caught within each period.

A number of one-tailed, two-sample *t*-tests were conducted under null hypotheses 1–4. Only cells that varied in one dimension were directly compared. (For example, under the hypothesis that mean sizes of fish from northern and southern waters did not differ, the mean lengths of pink salmon in the inside waters of northern and southern Southeast Alaska in August 1983 could be compared because the difference between these two cells was in only one dimension—north versus south.) Each possible pairwise comparison under one of the hypotheses was treated as a separate, single, and independent test, and all comparisons were equally weighted. No *t*-tests could be conducted if one cell had only one fish length. For the overall probability statement, the following statistic was used (Winer, 1971):

$$\chi^2 = 2\sum u_i, \text{ where } u_i = -\ln P_i.$$

Under the hypothesis that the observed probabilities were a random sample from a population of probabilities having a mean of 0.50, the χ^2 statistic has a sampling distribution which is approximated by the χ^2 distribution having $2k$ degrees of freedom, where k is the number of comparisons (Winer, 1971).

For size hypothesis 5 (no difference in mean fork length among salmon species), ANOVA was applied by pooling observations for each species from all habitats and regions. In effect, the pooled species length distribution is a weighted sum of the component distributions represented by the individual samples. Mean lengths of different species were compared separately for each period. If the overall *F*-test was significant, all possible species comparisons within a period were tested with two-tailed *t*-tests. Experimentwise error was controlled at α = 0.05 by adjusting the critical value for each *t*-test to α = 0.0085, by using the Dunn-Sidak method (Sokal and Rohlf, 1981).

Results

Total catch

Over 10,000 juvenile Pacific salmon were captured in 252 seine sets during the three sampling periods (Table 1). The catch consisted of 66% pink salmon, 11% chum salmon, 12% sockeye salmon, 10% coho salmon, and 1% chinook salmon. Pink salmon were the most abundant species (CPUE=27), with 6,804 caught. Chinook salmon were the least abundant species (CPUE=0.23), with only 57 caught.

Statistical distribution of catch

Catch distribution of juvenile salmon was extremely patchy. None were caught in 22% of the sets; more than half were captured in 5% of the sets. Plotting catch abundance against quantiles illustrated that the underlying statistical distribution for each species was clustered around zero (Fig. 2). Chinook salmon had the lowest FO in catches (12%), followed by sockeye salmon (32%), chum salmon (39%), pink salmon (45%), and coho salmon (54%). Coho salmon (median catch=1) was the only species with a median catch >0.

Juvenile salmon had highly aggregated distributions. Morisita's Index of Aggregation (I_δ) was significantly (P<0.001) greater than 1, indicating all species had aggregated distributions in each habitat and for all habitats pooled (Table 2).

Species associations

Pink, chum, and sockeye salmon catches were closely associated with each other. Catches of pink, chum, and sockeye salmon were positively and significantly (P<0.05) correlated (Table 3). In contrast, coho salmon abundance was not correlated with that of other salmon (Table 3).

Abundance

By habitat In Southeast Alaska and British Columbia combined, pink salmon were the most abundant species in each habitat (Table 1). The total pink salmon catch exceeded the catch of each of the other species by six times or more.

In Southeast Alaska, the CPUE of juvenile pink, chum, coho, and chinook salmon was greater in inside waters than in outside waters (Fig. 3), whereas sockeye salmon were more abundant in outside waters than inside waters (Fig. 3). For each species, the lowest CPUE and FO were in the outer coast inlets; sockeye salmon were never captured in an outer coast inlet (Fig. 3). The FO of pink, chum, and sockeye salmon was higher in outside than inside waters; the opposite was true for coho salmon (Fig. 3).

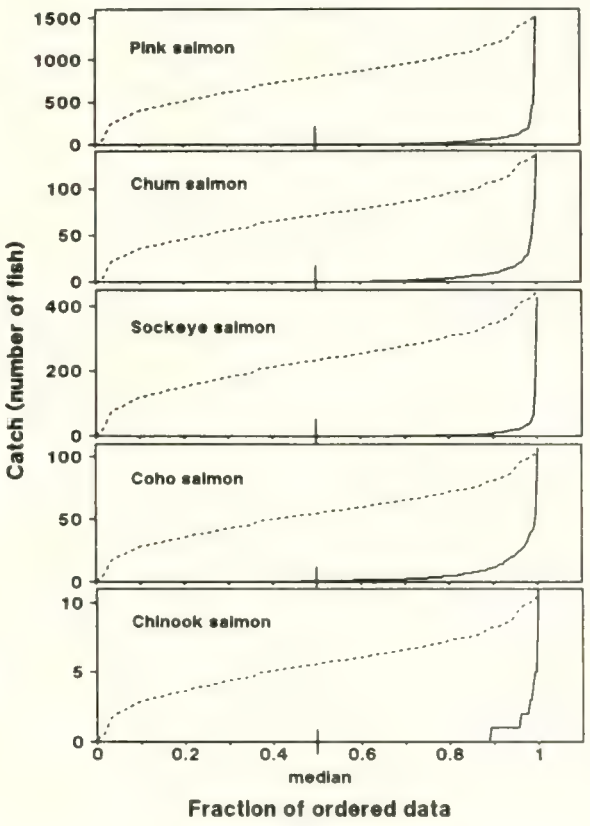

Figure 2

Quantile plots of abundance of the five species of juvenile Pacific salmon (pink, *Oncorhynchus gorbuscha*; chum, *O. keta*; sockeye, *O. nerka*; coho, *O. kisutch*; chinook, *O. tshawytscha*) caught in 252 purse-seine sets in Southeast Alaska in 1983 and 1984 and in British Columbia in 1984. The ranked catches are from the smallest (0) to largest (1) on the *X* axis. A theoretical normal distribution is indicated by the dotted lines.

By distance offshore in outside waters Distribution of juvenile salmon varied by distance offshore. Substantial numbers of fish were captured up to the maximum distance fished offshore (74 km, Fig. 4A). At intervals offshore, abundance and presence of each species is shown by the 3RSSH smoothed (Tukey, 1977) natural logarithms (ln) of CPUE (Fig. 4B) and smoothed FO (Fig. 4C) respectively. Highest ln CPUE of pink and chum salmon was near the center of the distance fished offshore (Fig. 4B). The transformed CPUE of sockeye salmon, the least abundant species nearshore (Fig. 4B), was greatest 37–74 km offshore, indicating they may have been abundant beyond 74 km. The ln CPUE of coho salmon suggests it was the least abundant species beyond 56 km (Fig. 4B).

Table 2

Morisita's Index of Aggregation (I_δ) and the associated *F*-value for seine catches of juvenile pink, chum, sockeye, and coho salmon taken in individual habitats (inside waters, outer coast inlets, outside waters) and all these habitats pooled in Southeast Alaska in August 1983, July and August 1984. Dashes indicate no fish captured.

Salmon species	Habitat	I_δ	*F*
Pink[1]	Inside waters	20.0	695.7*
	Outer coast inlet	10.7	153.0*
	Outside waters	3.6	54.9*
	All habitats pooled	18.5	474.5*
Chum[2]	Inside waters	13.6	66.6*
	Outer coast inlet	9.0	18.7*
	Outside waters	5.4	15.3*
	All habitats pooled	12.7	47.6*
Sockeye[3]	Inside waters	11.8	22.7*
	Outer coast inlets	—	—
	Outside waters	15.1	23.2*
	All habitats pooled	9.5	24.2*
Coho[4]	Inside waters	4.4	25.1*
	Outer coast inlets	2.9	3.1*
	Outside waters	7.8	19.5*
	All habitats pooled	6.2	24.3*

* *F*-value is significant for $P < 0.001$.
[1] *Oncorhynchus gorbuscha.*
[2] *O. keta*
[3] *O. nerka*
[4] *O. kisutch.*

Table 3

Spearman's rank correlation coefficient (ρ) test of pair rankings of juvenile salmon species catches taken during 252 separate sets in Southeast Alaska and British Columbia.

Comparison of species of salmon	Correlation between species pair rankings (ρ)
Pink[1]/Chum[2]	+0.75*
Pink/Sockeye[3]	+0.68*
Pink/Coho[4]	+0.14
Chum/Sockeye	+0.55*
Chum/Coho	+0.13
Sockeye/Coho	+0.11

* Significant association at $P < 0.05$, with rejection criteria adjusted for multiple comparisons.
[1] *Oncorhynchus gorbuscha.*
[2] *O. keta.*
[3] *O. nerka.*
[4] *O. kisutch*

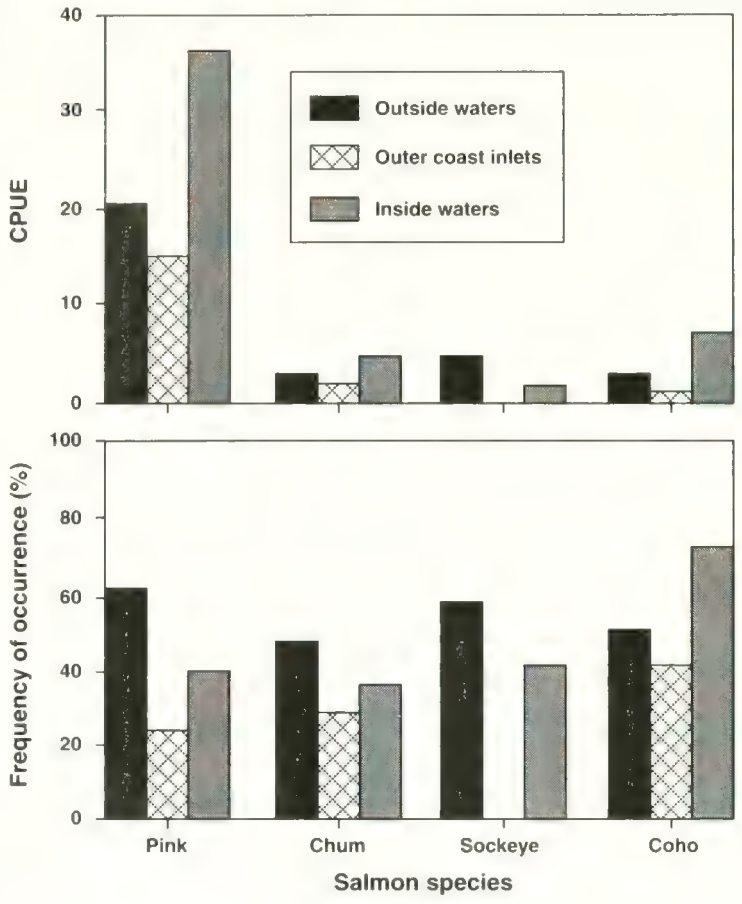

Figure 3

Catch per unit of effort (CPUE) and frequency of occurrence of juvenile salmonids (pink, *Oncorhynchus gorbuscha*; chum, *O. keta*; sockeye, *O. nerka*; coho, *O. kisutch*; in outside waters (77 sets), outer coast inlets (45 sets), and inside waters (109 sets) in Southeast Alaska in 1983 and 1984 combined.

Pink and chum salmon FO was lowest nearshore, then increased and stabilized mid-distance offshore, around 37 km (Fig. 4C). Pink salmon were caught in all sets beyond 37 km and had the highest FO of all species; sockeye salmon FO remained constant 2–74 km offshore. Coho salmon FO was the highest nearshore (2 km) of all species, then the FO stabilized at 37 km and beyond (Fig. 4C).

By sampling period Abundance of juvenile salmon in Southeast Alaska increased from July (CPUE=11) to August (CPUE=58) 1984 for all species. Summed over all habitats, pink, chum, sockeye, and coho salmon had higher FO's and abundance in August than in July. In outside waters, CPUE of each species increased two to seven times from July to August 1984, with juvenile pink salmon showing the largest increase (Fig. 5). In inside waters, CPUE of pink and chum salmon increased 10 and 5 times respectively from July to August, whereas CPUE's of sockeye and coho salmon remained constant (Fig. 5). For all four species, FO increased in outside waters but decreased in inside waters from July to August 1984 (Fig. 5). The low number of sets (four) made in outer coast inlets of Southeast Alaska in August 1984 precluded seasonal comparisons of CPUE or FO for this habitat.

Size

Juvenile salmon were larger in outside waters than in inside waters. Thirteen matched pairs of size samples could be compared under the hypothesis that size did not vary between outside and inside waters; the fish were larger in the outside water in all comparisons (Table 4, χ^2=133.66, df=26, P<0.005) and the null hypothesis was rejected.

Juvenile salmon in outside waters were larger farther seaward. Of the eight possible matched pairs of samples compared under the hypothesis that size was not different between outside waters >37 km offshore and ≤37 km offshore, the juvenile salmon were larger >37 km seaward in all comparisons (Table 4, χ^2=67.44, df=16, P<0.005).

Juvenile salmon in northern waters were larger than those in southern waters. The fish were larger in the northward locations than southward locations in 18 of 23 possible paired size comparisons (Table 4, χ^2=214.76, df=46, P≤0.005).

Juvenile salmon were larger in August than in July. Of the matched size samples compared under the hypothesis that size was not different between August and July of 1984, fish in August were larger than in July in 10 of 12 comparisons (Table 4, χ^2=145.36, df=24, P<0.005).

The sizes between the different species of juvenile Pacific salmon differed significantly (P<0.05) (Table 5). Coho salmon juveniles were significantly larger than other species in each sampling period; mean length of coho salmon was always at least 40% greater than in other species, whereas pink, chum, and sockeye salmon were within 9% of each other. Juvenile sockeye salmon were significantly larger

than pink salmon in each sampling period and were significantly larger than chum salmon in 1984. In both July and August 1984, pink and chum salmon did not differ in size, and in August 1983 chum and sockeye salmon did not differ in size.

Discussion

Fish distribution

Each species of juvenile salmon was highly aggregated rather than dispersed randomly. In contrast to our results, Hartt and Dell (1986) seldom observed zero catches and therefore concluded that juvenile salmon in the ocean were evenly dispersed. Several differences between our study and theirs may explain the differing conclusions. Seines used by Hartt and Dell were longer than ours and were held open for 30 minutes instead of 3–5 minutes. Our catches may be more of a point estimate or instantaneous picture of fish abundance, whereas their seines were more likely to intercept at least part of a juvenile salmon school. More importantly, Hartt and Dell did not separate juvenile salmon by species when considering their distribution.

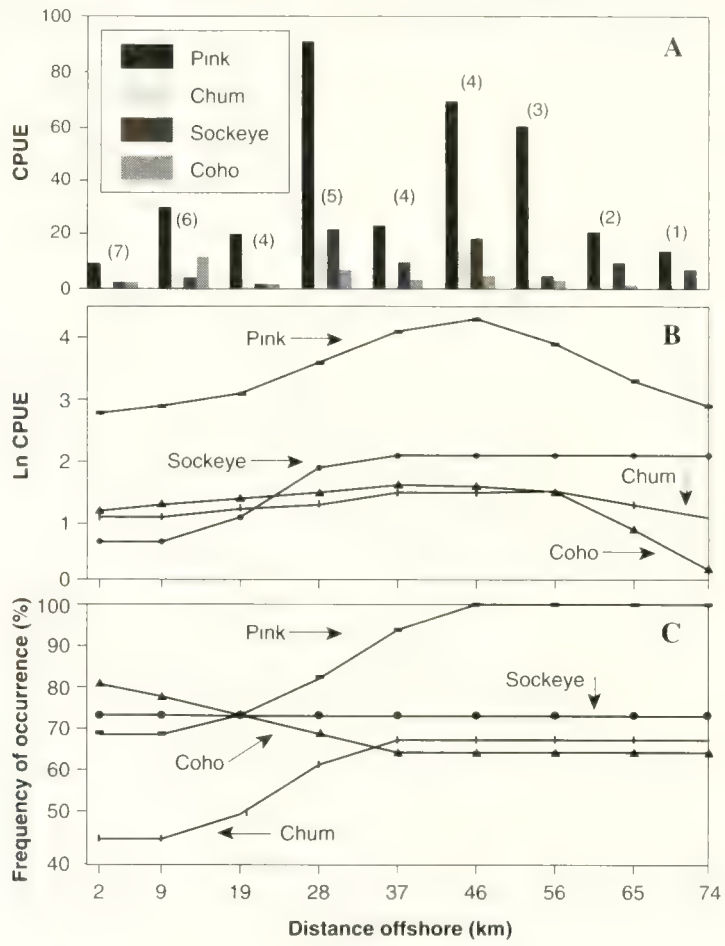

Figure 4

Abundance of juvenile salmonids (pink, *Oncorhynchus gorbuscha*; chum, *O. keta*; sockeye, *O. nerka*; coho, *O. kisutch*) by distance offshore in the outside waters of Southeast Alaska in August 1984 (36 sets). Abundance is shown in terms of (**A**) catch per unit of effort (CPUE), (**B**) the smoothed natural logarithm of CPUE, and (**C**) the smoothed frequency of occurrence of the catches; number of sets is in parentheses. All distances are rounded to the nearest kilometer. Actual distance between intervals (except the first) is 9.3 km.

Species associations

Juvenile pink, chum, and sockeye salmon were generally closely associated with each other in their distribution. The distribution of these species, however, differed from the distribution of coho salmon, a result consistent with the conclusions of Hartt and Dell (1986) and Waddell et al. (1989). In the inside waters and outer coast inlets, we found that pink, chum, and sockeye salmon had a lower FO than coho salmon, indicating that those species were more highly aggregated and sparsely distributed than coho salmon. Paszkowski and Olla (1985) found that behavior patterns of juvenile coho salmon promoted dispersion, not aggregation. The utilization of similar areas in this study by juvenile pink, chum, and sockeye salmon correlates with the high degree of diet overlap observed between these species; in contrast, juvenile coho salmon showed little diet overlap with the other species.[1] Healey (1991) reported that juvenile pink, chum, and sockeye salmon in British Columbia were also aggregated.

Migration

The migration of juvenile salmon off Southeast Alaska (Hartt and Dell, 1986) consists of two components: 1) fish migrating north from the Pacific Northwest and British Columbia, and 2) fish from Southeast Alaska migrating from inside to outside waters.

[1] J. H. Landingham, Auke Bay Laboratory, 11305 Glacier Highway, Juneau, AK 99801–8626, pers. commun. Jan. 1992.

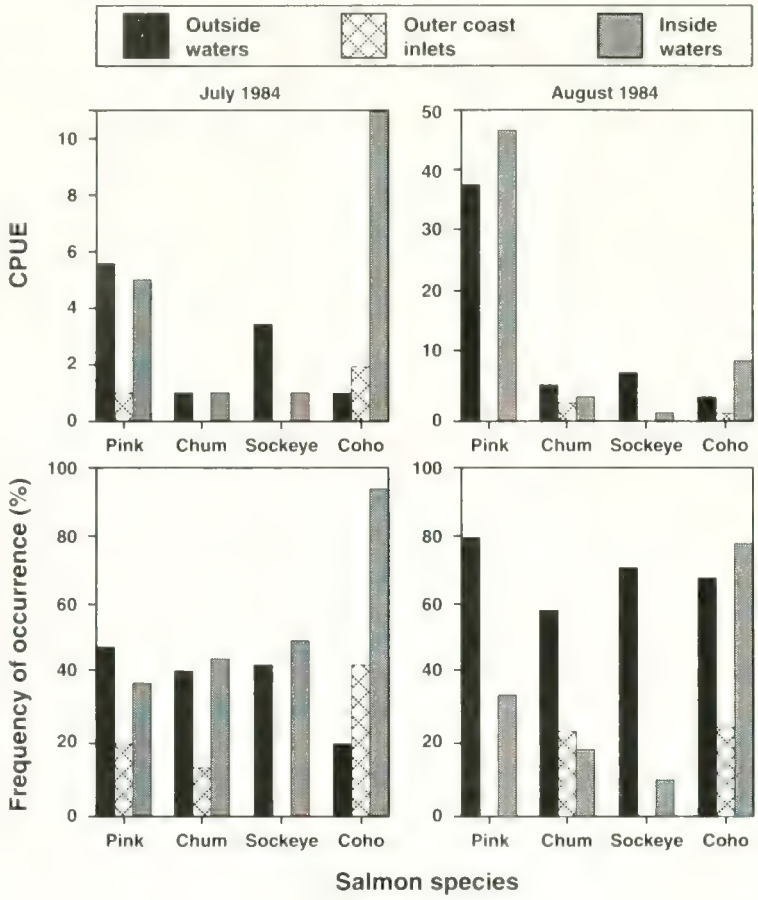

Figure 5

Catch per unit of effort (CPUE) and frequency of occurrence of juvenile salmonids (pink, *Oncorhynchus gorbuscha*; chum, *O. keta*; sockeye, *O. nerka*; coho, *O. kisutch*) in the outside waters (69 sets), outer coast inlets (18 sets), and inside waters (55 sets) in Southeast Alaska in July and August 1984. Note change in scale of CPUE from July to August 1984.

Juvenile salmon migrations along the Pacific coast in 1984 did not peak off Southeast Alaska until, at earliest, August. In July, CPUE's were much higher in the outside waters of British Columbia than in Southeast Alaska. By August, CPUE of juvenile salmon in outside waters of Southeast Alaska had increased fivefold, and FO had increased for each species. Hartt and Dell (1986) observed that juvenile salmon abundance peaked in August in outside waters of Southeast Alaska.

In Southeast Alaska, juvenile sockeye salmon probably begin their ocean migration to the Gulf of Alaska before juvenile pink and chum salmon, based on two observations from our study. First, the sockeye salmon did not occur in protected waters along the outer coast of Southeast Alaska like the other species: no sockeye salmon were captured in an outer coast inlet. Second, sockeye salmon was the only species with a higher CPUE in outside waters than in inside waters. This higher abundance outside, coupled with low abundance in inside waters in July and August, is consistent with the conclusion that sockeye salmon commence their ocean migration before pink or chum salmon (Straty, 1981; Healey, 1982).

The migration of pink salmon from the inside waters of Southeast Alaska lasts until at least September. Martin (1966) concluded that late July and early August were the peak periods of juvenile pink salmon migration from the inside waters. However, our data show that pink salmon abundance in inside waters increased from July to August and that pink salmon were more abundant in inside waters than outside waters in August, thus indicating that migration out of the inside waters was not complete in August. The seasonal migration of juvenile chum salmon out of Southeast Alaska could not be determined from the abundance data of this study. The migration of juvenile pink, chum, and sockeye salmon out of the inside waters in September and later has not been studied.

The offshore migration of coho salmon in Southeast Alaska is more complex. CPUE and FO of coho salmon in inside waters remained relatively constant for July and August. Coho salmon was the only species with both a higher CPUE and FO in inside waters than in outside waters in August. These data suggest extensive residency in inside waters for a substantial portion of coho salmon juveniles in Southeast Alaska. Other researchers have found that some juvenile coho salmon remain in the eastern Pacific Ocean inside waters until late fall (Healey, 1984; Hartt and Dell, 1986; Orsi et al., 1987). Winter residency of juvenile coho in inside waters of Southeast Alaska is apparently rare.[2] Hartt and Dell (1986) and Pearcy and Fisher (1990) also found coho salmon offshore as early as May or June; Hartt and Dell (1986) noted that juvenile coho salmon migrated seaward earlier than the other salmon species, presumably because of their larger

[2] J. A. Orsi, Auke Bay Laboratory, 11305 Glacier Highway, Juneau, AK 99801-8626, pers. commun. Jan. 1992.

Table 4

Fork length (FL) of juvenile salmonids sampled by period, habitat, north (N) or south (S) region, and distances offshore in outside waters of Southeast Alaska in 1983 and 1984 and outside waters of British Columbia (B.C.) in 1984. Values are mean ± standard error, with number of samples in parenthesis. In brackets under the values are the specific paired size comparisons used in the null hypothesis testing of sizes by: northern vs. southern waters (A1, A2, ..., A23); outside vs. inside waters (B1, B2, ..., B13); August vs. July 1984 (C1, C2, ..., C12); and outside waters >37 km offshore vs. outside waters <37 km offshore (D1, D2, ..., D8). Dashes indicate no fish caught.

		FL of salmon (mm)			
Period	Habitat (region)	Pink[1]	Chum[2]	Sockeye[3]	Coho[4]
Aug 83	Inside (N)	169 ± 0.8 (890) [A1]	180 ± 1.8 (199) [A2]	163 ± 2.7 (74)	233 ± 1.8 (136) [A3]
	Inside (S)	121 ± 1.9 (10) [A1, B1]	139 ± 4.6 (18) [A2, B2]	—	227 ± 11.9 (5) [A3, B3]
	Outer coast inlet (N)	—	166 ± 4.9 (4) [A4]	—	221 ± 6.3 (11) [A5]
	Outer coast inlet (S)	124 ± 0.5 (404)	133 ± 1.5 (76) [A4]	—	217 ± 7.9 (11) [A5]
	Outside (S)	153 ± 3.6 (19) [B1]	141 ± 13.5 (2) [B2]	152 ± 2.6 (9)	234 ± 3.6 (25) [B3]
July 84	Inside (N)	121 ± 1.7 (94) [A6, B4, C1]	112 ± 5.2 (19) [B5, C2]	136 ± 5.9 (20) [B6, C3]	193 ± 2.0 (206) [A7, B7, C4]
	Inside (S)	132 ± 1.2 (3) [A6, B8]	135 ± 0 (1)	—	202 ± 7.8 (3) [A7, B9]
	Outer coast inlet (N)	105 ± 10.9 (4)	139 ± 0 (1)	—	177 ± 3.6 (27)
	Outside (N)	135 ± 0.8 (207) [A8, A9, B4, C5]	133 ± 2.3 (38) [A10, A11, B5, C6]	151 ± 2.1 (111) [A12, A13, B6, C7]	220 ± 4.5 (26) [A14, A15, B7, C8]
	Outside (S)	134 ± 4.6 (10) [A8, A16, B8, C9]	161 ± 18.5 (2) [A10, A17, C10]	157 ± 2.6 (19) [A12, A18, C11]	224 ± 7.5 (8) [A14, A19, B9, C12]
	Outside (B.C.)	128 ± 1.0 (126) [A9, A16]	132 ± 1.5 (46) [A11, A17]	128 ± 0.9 (197) [A13, A18]	129 ± 10.3 (7) [A15, A19]
Aug 84	Inside (N)	143 ± 1.0 (358) [B10, C1]	125 ± 1.2 (118) [B11, C2]	157 ± 2.1 (18) [B12, C3]	234 ± 1.9 (168) [B13, C4]
	Outer coast inlet (S)	—	132 ± 6.1 (12)	—	246 ± 12.2 (3)
	Outside (N)	144 ± 0.6 (730) [A20, B10, C5]	160 ± 2.0 (93) [A21, B11, C6]	159 ± 1.5 (75) [A22, B12, C7]	267 ± 5.6 (33) [A23, B13, C8]
	≤37 km	143 ± 0.8 (457) [D1]	157 ± 2.2 (73) [D2]	156 ± 1.7 (52) [D3]	266 ± 6.5 (28) [D4]
	>37 km	146 ± 1.0 (273) [D1]	169 ± 4.1 (20) [D2]	165 ± 2.8 (23) [D3]	274 ± 2.3 (5) [D4]
	Outside (S)	139 ± 1.0 (373) [A20, C9]	144 ± 2.1 (66) [A21, C10]	149 ± 0.9 (141) [A22, C11]	265 ± 3.3 (37) [A23, C12]
	≤37 km	135 ± 1.2 (243) [D5]	144 ± 2.7 (38) [D6]	148 ± 1.0 (103) [D7]	263 ± 3.3 (35) [D8]
	>37 km	144 ± 1.4 (130) [D5]	145 ± 3.5 (28) [D6]	152 ± 1.5 (38) [D7]	291 ± 15.0 (2) [D8]

[1] *Oncorhynchus gorbuscha.*
[2] *O. keta.*
[3] *O. nerka.*
[4] *O. kisutch.*

size. An early component of coho salmon juveniles could have moved offshore in June, prior to our sampling effort. More extensive sampling from late spring through fall is required to define the timing of migrations of coho salmon in the waters of Southeast Alaska.

The sizes of juvenile salmon we captured support the findings of Hartt and Dell (1986) that fish in more northern locations have been at sea longer than those in southern locations. Hartt and Dell (1986) observed a general increase in mean length of juvenile salmon from south to north in the outside waters from Washington to Southeast Alaska. In the coastal waters off Oregon and Washington, larger, presumably older, juvenile coho salmon were found farther north (Pearcy and Fisher, 1988). Assuming they were similar in size on entering the sea, the smaller fish in the southerly locations are recent arrivals from nearby production areas, whereas the larger fish in the northerly locations have been at sea longer and probably migrated from more southerly production areas (Hartt and Dell, 1986). Our studies also reveal juvenile salmon in Southeast Alaska were larger in the outside waters than inside waters and farther offshore in the outside waters than closer to shore. The progression of juvenile salmon migrations over a season may be size-dependent (Healey, 1982, 1984), and certain phases of migration may depend on fish reaching a threshold size. According to Hartt and Dell (1986), the offshore migration into the Gulf of Alaska of juvenile pink, chum, and sockeye salmon does not begin until September or October when fish are 180–230 mm or greater in mean FL. However, our findings show that these species are found offshore earlier (in August) and at a much smaller size (145–170 mm mean FL).

Width of migration band

Juvenile Pacific salmon typically migrate in nearshore waters during their first few months at sea (Straty, 1981); however, the width of this migration band varies regionally (Straty and Jaenicke, 1984; Hartt and Dell, 1986). Juvenile salmon concentrated within 37 km of shore along the broad continental shelf (<183 m deep) off Oregon and Washington (Miller et al., 1983; Pearcy and Fisher, 1990). Hartt and Dell (1986) concluded that the band of juvenile salmon was within 37 km of shore off Southeast Alaska where the continental shelf is narrow, but that the band widened in the northern Gulf of Alaska where the shelf is wider.

Our results indicate that the coastal band of migrating juveniles can be much wider than 37 km and that the offshore migration beyond 37 km may begin as early as August. Catches of juvenile salmon 74 km offshore—the maximum distance we fished offshore—and the catch distributions indicate that some juvenile salmon (pink, chum, and sockeye) may have been abundant even farther seaward. Two-thirds of the juvenile salmon captured in outside waters in August 1984 were beyond the continental shelf.

The width of the migration band is probably influenced by the Alaska Coastal Current—a dominant feature in the circulation of Gulf of Alaska coastal waters. This freshwater-driven current begins along the British Columbia coast and flows north then west within 20 km of shore into the Bering Sea (Royer, 1984). The strength of this current is affected by local precipitation, wind, air temperature, and other meteorological conditions. Millions of juvenile salmon migrate through the current every year en route to more oceanic waters. Cooney (1984) theorized that the current represents a critical early-feeding habitat in the summer and early fall. In modeling the early-ocean limitations of Pacific salmon production, Wal-

Table 5

Comparison of mean fork lengths (FL) of juvenile salmonids caught in the marine waters (all habitats pooled) of Southeast Alaska and northern British Columbia in 1983–84. Sample size = n; standard deviation of the size in mm = s. The hypothesis was that there were no size differences between species during the same period. The rejection criteria were adjusted for multiple comparisons so that experimental error did not exceed $\alpha = 0.05$. Species having the same letter in a column were not significantly different by size.

	August 1983			July 1984			August 1984		
Salmon species	n	mean FL (mm)	s	n	mean FL (mm)	s	n	mean FL (mm)	s
Pink[1]	1,323	155[c]	29	444	130[c]	14	1,461	142[c]	18
Chum[2]	299	165[b]	31	108	129[c]	17	289	141[c]	22
Sockeye[3]	83	162[b]	23	347	138[b]	20	234	153[b]	12
Coho[4]	188	232[a]	22	277	193[a]	30	241	253[a]	20

[1] *Oncorhynchus gorbuscha*.
[2] *O. keta*.
[3] *O. nerka*.
[4] *O. kisutch*.

ters et al. (1978) noted that production predictions were critically sensitive to the width of the coastal band within which salmon migrate during their first summer at sea. We recommend additional sampling be conducted from June through September to better document 1) the width of the coastal band of juvenile salmon migrations through the summer and 2) the timing of offshore migrations beyond 37 km from the outer coast.

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Literature cited

Bax, N. J.
1983. Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) released into Hood Canal, Puget Sound, Washington, in 1980. Can. J. Fish. Aquat. Sci. 40:426–435.

Browning, R. J.
1980. Fisheries of the North Pacific: history, species, gear and processes. Alaska Northwest Publ., Anchorage, 423 p.

Chambers, J. M., W. S. Cleveland, B. Kleiner, and P. A. Tukey.
1983. Graphical methods for data analysis. Duxbury Press, Boston, 395 p.

Cooney, R. T.
1984. Some thoughts on the Alaska Coastal Current as a feeding habitat for juvenile salmon. *In* W. G. Pearcy (ed.), The influence of ocean conditions in the production of salmonids in the North Pacific, p. 256–268. Oregon State Univ. Sea Grant College Program Rep. ORESU-W-83–001.

Daniel, W. W.
1978. Applied nonparametric statistics. Houghton Mifflin, Boston, 503 p.

Furnell, D. J., and J. R. Brett.
1986. Model of monthly marine growth and natural mortality for Babine Lake sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 43:999–1004.

Godfrey, H., K. A. Henry, and S. Machidori.
1975. Distribution and abundance of coho salmon in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 31, 80 p.

Hartt, A. C.
1975. Problems in sampling Pacific salmon at sea. *In* Symposium on evaluation of methods of estimating the abundance and biological attributes of salmon on the high seas, p. 165–231. Int. North Pac. Fish. Comm. Bull. 32.

Hartt, A. C., and M. B. Dell.
1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. Int. North Pac. Fish. Comm. Bull. 46:1–105.

Healey, M. C.
1982. The distribution and residency of juvenile Pacific salmon in the Strait of Georgia, British Columbia, in relation to foraging success. *In* B. R. Melteff and R. A. Nevé (eds.), Proceedings of the North Pacific aquaculture symposium, p. 61–69. Alaska Sea Grant Rep. 82–2. Univ. Alaska, Fairbanks.
1984. The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* W. J. McNeil and D. C. Himsworth (eds.), Salmonid ecosystems of the North Pacific, p. 203–229. Oregon State Univ. Press, Corvallis.
1991. Diets and feeding rates of juvenile pink, chum, and sockeye salmon in Hecate Strait, British Columbia. Trans. Am. Fish. Soc. 120:303–318.

Manzer, J. I.
1964. Preliminary observations on the vertical distribution of Pacific salmon (Genus *Oncorhynchus*) in the Gulf of Alaska. J. Fish. Res. Board Can. 21:891–903.

Martin, J. W.
1966. Early sea life of pink salmon. *In* W. L. Sheridan (ed.), Proceedings of the 1966 Northeast Pacific pink salmon workshop, p. 111–125. Alaska Dep. Fish Game, Info. Leafl. 87, Juneau.

Miller, D. R., J. G. Williams, and C. W. Sims.
1983. Distribution, abundance and growth of juvenile salmonids off the coast of Oregon and Washington, summer 1980. Fish. Res. 2:1–17.

Morisita, M.
1959. Measuring the dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu Univ. Ser. E. (Biol) 2:215–235.

Orsi, J. A., A. G. Celewycz, D. G. Mortensen, and K. A. Herndon.
1987. Sampling juvenile chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) by small trolling gear in the northern and central regions of southeastern Alaska, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-115, 47 p.

Parker, R. R.
1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25:757–794.

Paszkowski, C.A., and B. L. Olla.
1985. Social interactions of coho salmon (*Oncorhynchus kisutch*) smolts in seawater. Can. J. Zool. 63:2401–2407.

Pearcy, W. G., and J. P. Fisher.
1988. Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean. Fish. Bull. 86:173–195.

1990. Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981–1985. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 93, 83 p.

Poole, R. W.
1974. An introduction to quantitative ecology. McGraw-Hill, NY, 532 p.

Royer, T. C.
1984. Annual and interannual variability of temperature and salinity in the Gulf of Alaska with emphasis on the coastal waters. *In* W. G. Pearcy (ed.), The influence of ocean conditions in the production of salmonids in the North Pacific, p. 244–255. Oregon State Univ. Sea Grant College Program Rep. ORESU-W-83–001.

Sokal, R. R., and F. J. Rohlf.
1981. Biometry, the principles and practices of statistics in biological research. W. H. Freeman & Co., NY, 859 p.

Straty, R. R.
1981. Trans-shelf movements of Pacific salmon. *In* D. W. Hood and J. A. Calder (eds.), The eastern Bering Sea shelf: oceanography and resources 1:575–595. U.S. Dep. Commer., NOAA, Off. Mar. Pollut. Assess., Juneau, AK.

Straty, R. R., and H. W. Jaenicke.
1984. Estuarine influence of salinity, temperature, and food on the behavior, growth, and dynamics of Bristol Bay sockeye salmon. *In* W. J. McNeil and D. C. Himsworth (eds.), Salmonid ecosystems of the North Pacific, p. 247–265. Oregon State Univ. Press, Corvallis.

Tukey, J. W.
1977. Exploratory data analysis. Addison-Wesley Publishing, Reading, MA, 506 p.

Waddell, B. J., M. C. Healey, and J. F. T. Morris.
1989. Data analysis of 1986 and 1987 Hecate Strait juvenile salmon surveys. Can. Tech. Rep. Fish. Aquat. Sci. 1719, 76 p.

Walters, C. J., R. Hilborn, R. M. Peterman, and M. J. Staley.
1978. Model for examining early ocean limitation of Pacific salmon production. J. Fish. Res. Board Can. 35:1303–1315.

Winer, B. J.
1971. Statistical principles in experimental design. McGraw-Hill, NY, 907 p.

Abstract.—Evidence supporting a two stock hypothesis for king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico was developed principally from the results of electrophoretic patterns of one polymorphic dipeptidase locus and supporting evidence from mark-recapture, charterboat catch, and spawning studies.

There are two identifiable stocks of king mackerel in the Gulf of Mexico: a western stock and an eastern stock. The western stock migrates northward along the Mexico-Texas coast during the spring and early summer from its winter grounds in Mexico (Yucatan Peninsula). This stock has a high frequency of the dipeptidase *PEPA-2*a* allele. The eastern stock migrates at the same time northward along the eastern coast of the Gulf of Mexico from its winter grounds in south Florida (Gulf of Mexico and Atlantic coast). This stock has a high frequency of the dipeptidase *PEPA-2*b* allele. Both stocks migrate simultaneously into the northern Gulf of Mexico and mix at varying degrees in the northern summering grounds (Texas to northwest Florida).

Evidence for distinct stocks of king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico

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The king mackerel, *Scomberomorus cavalla*, is a widely distributed, coastal pelagic species in the western Atlantic Ocean. This scombrid is found from the Gulf of Maine to Rio de Janiero, Brazil, including the Gulf of Mexico and Caribbean Sea (Rivas, 1951; Collette and Nauen, 1983). It is a valuable resource that supports fisheries throughout most of its range (Manooch et al., 1978).

The U.S. and Mexico have been major exploiters of king mackerel resources. U.S. commercial landings have been reported since 1888. Landings have ranged from 2,213 metric tons (t) (1972) to 4,746 t (1974). U.S. recreational catches are estimated to be two to ten times larger than the commercial catches (Deuel and Clark, 1968; Deuel, 1973; Manooch, 1979; U.S. Dep. Commer., 1984, 1986, 1987). In Mexican waters, commercial landings for king mackerel from 1968 to 1988 have ranged from 784 t (1968) to 6,133 t (Collins and Trent, 1982[1]).

Because king mackerel are presently managed in the southeastern U.S. (represented by more than eight states and two regional fishery management council jurisdictions) and support both recreational and mixed gear commercial fisheries, the identities of component stocks are important. Current management of king mackerel fisheries assumes two migratory stocks with overlapping ranges, one in the U.S. Atlantic Ocean and one in the Gulf of Mexico (Gulf of Mexico and South Atlantic Fishery Management Councils, 1985). This separation is based on mark-recapture results (Sutherland and Fable, 1980; Williams and Godcharles, 1984[2]; Sutter et al., 1991).

The concept of a stock is one of the most fundamental to fishery management. A stock is variously defined, ranging from the strict definition of a single interbreeding population to a unit capable of in-

[1] L. A. Collins and L. Trent, Natl. Mar. Fish. Serv., Panama City, FL, pers. commun. 1992.

[2] Williams, R. O., and M. F. Godcharles. 1984. Completion report, king mackerel tagging and stock assessment. Project 2–341–R. Fla. Dep. Natl. Resour. Unpubl. Rep., 45 p.

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dependent exploitation or management and containing as much of an interbreeding unit or as few reproductively isolated units as possible (Royce, 1972). An additional term that has been used to define the stock concept used in fishery management is "unit stock" which was referred to by Kutkuhn (1981) as "one consisting of randomly interbreeding members whose genetic integrity persists whether they remain spatially and temporally isolated as a group, or whether they alternately segregate for breeding and otherwise mix freely with members of other unit stocks of the same species." This term is more functional for application to many marine resources which have identifiable components but for which reproductive isolation has not been demonstrated. We consider stock and unit stock to be identical with regard to king mackerel resources at the present time.

Using Kutkuhn's (1981) definition, this report presents evidence of two stocks of king mackerel existing in the Gulf of Mexico (the Gulf), an eastern and a western stock which winter off south Florida and off the Yucatan peninsula (Mexico), respectively. In the spring these fish migrate along their respective coasts to summer areas in the northern Gulf. The concept of two Gulf of Mexico stocks was first presented by Baughman (1941). He based his hypothesis on observations by fishermen of simultaneous migrations along the eastern and western sides of the Gulf. More recently, May (1983)[3] reported electrophoretic differences in king mackerel between the eastern and western Gulf. Using more recent tagging data and electrophoretic information, Grimes et al. (1987) reintroduced the hypothesis.

Additional evidence for a two-stock hypothesis is the following:

1 Fish movements along the coast, as indicated by mark-recapture studies (Fable et al., 1990[4]).
2 The simultaneous migration along the eastern and western coasts of the Gulf in spring and early summer as detected by analysis of charterboat CPU data (Trent et al., 1987b).
3 The difference in spawning times of king mackerel in the northern and southern areas of the Gulf (Grimes et al., 1990).

We report the results from electrophoretic investigations and summarize current information from tagging, migration, and spawning time studies. We also propose a possible mechanism to explain the observed results with regard to the water circulation of the area.

Methods and materials

Samples of muscle tissue, along with fork length (mm) and sex, were collected during 1985 through 1990 from fish obtained in recreational and commercial fisheries from North Carolina to Yucatan (Table 1). The samples were frozen as soon as possible in the field and then shipped frozen to the National Marine Fisheries Service's Panama City Laboratory. Muscle tissue (about 10 grams) was excised from each sample and stored in a freezer (in 1985 at –5° to –10°C and from 1986 through 1990 at –100°C).

Tissue extracts were prepared by mixing equal volumes of muscle tissue and distilled water and grinding with glass rods to uniform pastes. Extracts were centrifuged at 3,400 rpm (1,000 × G) for five minutes, then supernatants were drawn onto 4 mm × 8 mm filter paper inserts (Whatman 1).

Starch gel electrophoretic separation of the extracts was performed following the methods of Kristjansson (1963). Electrophoretic buffers were those of A) Markert and Faulhaber (1965), and B) N-(3–aminopropyl)-morpholine-citrate (pH 6.1) buffer of Clayton and Tretiak (1972). The gel consisted of 35 g of starch (Sigma Chemical Co. lots 123F-0591, 35K-0383, and 94F-0536) plus 250 mL of buffer. Amperage during electrophoresis was kept below 50 MA, and voltage varied between 100 and 400 V, depending on the buffer. Temperature was maintained at 2°C by using a refrigerated cooling system (see Aebersold et al., 1987, for description). After electrophoresis, the gels were sliced into four horizontal sections and stained for dipeptidase (EN 3.4.-.-). In 1985 (1,223 fish) and 1988 (879 fish), 27 additional enzymes were examined. Methods followed May (1983)[3] and Aebersold et al. (1987).

We conducted statistical analyses using Biosys-1 (Swofford and Selander, 1981) to test for conformance to Hardy-Weinberg expectations and spatially related differences in allele frequencies compared to distance and physical feature subdivisions. The Kolmogorov-Smirnov goodness-of-fit test was used for comparing allele distributions by size of fish (100–mm-FL intervals), while the chi-square contingency test was used for comparing allele distributions by sex (see Sokol and Rohlf (1981) for procedures).

[3] May, B. 1983. Genetic variation in king mackerel (*Scomberomorus cavalla*). Final Rep. Fla. Dep. Natl. Resour. Contract C-14–34, 20 p.

[4] Fable, Jr., W.A., J. Vasconcelos P., K. M. Burns, H. R. Osburn, L. Schultz R., and S. Sanchez G. (1990). King mackerel, *Scomberomorus cavalla*, movements and migrations in the Gulf of Mexico. Natl. Mar. Fish. Serv., Panama City Lab., Panama City, FL (unpubl. ms.).

Table 1

King mackerel (*Scomberomorus cavalla*) *dipeptidase-2*a* allele frequencies by state for each month and year.

	Month[1]												
State and year	1	2	3	4	5	6	7	8	9	10	11	12	Total
Gulf of Mexico													
Florida[2]													
1985		0.050(26)				0.012(83)	0.132(32)		0.034(29)				0.041(170)*
1986							0.107(28)		0.93(43)				0.099(71)
1987				0.000(8)	0.000(24)	0.257(191)*		0.000(31)	0.085(106)				0.161(360)*
1988				0.000(8)		0.138(40)*	0.017(64)		0.033(75)	0.167(21)			0.072(208)*
1989	0.174(23)				0.160(53)		0.026(39)	0.100(115)*	0.159(148)*	0.159(148)*			0.128(378)*
1990	0.677(12)		0.167(9)	0.000(4)	0.042(24)*	0.125(88)	0.402(61)*	0.182(22)					0.227(220)*
Alabama													
1986							0.186(35)		0.038(26)				0.123(61)
1987					0.159(44)*	0.179(14)	0.468(77)		0.380(83)*				0.353(218)*
1988							0.920(88)						0.920(88)
1989								0.688(8)					0.688(8)
1990							0.306(18)						0.306(18)
Mississippi													
1986							0.684(38)	0.147(17)	0.,788(14)				0.551(69)*
1987						0.579(19)			0.564(47)				0.568(66)
1988						0.935(23)	0.750(32)		0.206(17)				0.671(72)*
1989									0.833(3)				0.833(3)
1990						0.500(9)*	0.333(13)	0.000(13)					0.250(34)*
Louisiana													
1985									0.040(25)	0.940(25)	0.477(22)	0.615(52)	0.536(124)*
1986							0.455(44)*	0.520(25)*				0.382(17)	0.459(86)*
1987	0.612(58)						0.541(148)	0.606(109)	0.633(64)				0.586(379)
1988							0.750(60)	0.306(18)					0.647(78)
1989							0.534(29)						0.534(29)
Texas (east)[3]													
1986							0.851(104)*	0.575(100)*					0.716(204)*
1987								0.606(113)					0.606(113)
1988							0.911(225)*						0.911(225)*
1989							0.814(110)*	0.902(132)					0.806(242)*
1990					0.000(1)	0.657(35)							0.639(36)
Texas (south)[3]													
1985					0.000(1)	0.657(35)							0.463(353)
1986					0.929(7)	0.515(67)	0.434(234)	0.353(17)	0.536(28)				0.777(146)
1987					0.457(47)	0.735(34)	0.655(103)	0.725(302)		0.810(42)			0.695(528)

Table 1 (Continued)

State and year	Month[1] 1	2	3	4	5	6	7	8	9	10	11	12	Total
Texas (south)[3] Continued													
1988					0.921(101)*	0.978(93)*	0.750(138)*	0.799(127)					0.847(459)*
1989				0.967(15)	0.911(84)*	0.963(41)	0.953(109)	0.833(24)	0.922(53)				0.934(324)*
1990				0.935(46)	0.667(3)	0.766(64)	0.836(61)						0.833(174)*
Veracruz, MX													
1985				0.031(16)									0.31(16)
1986				0.910(100)*		0.896(91)		0.600(70)					0.822(261)
1987				0.801(187)									0.801(187)
1988				0.810(77)									0.810(77)
1989			0.883(192)*										0.883(192)*
1990			0.969(128)*										0.969(128)*
Yucatan, MX													
1986		0.447(76)						0.778(18)					0.511(94)*
1987				0.716(76)									0.716(76)
1988			0.670(100)*										0.670(100)*
1990			0.846(159)*										0.846(159)*
Atlantic Coast Florida													
1985		0.017(60)				0.010(50)	0.040(161)						0.037(271)*
1986						0.000(15)	0.034(104)	0.067(15)					0.034(134)
1987				0.031(16)	0.063(16)								0.047(32)
1988					0.67(45)	0.158(19)		0.079(19)				0.125(20)	0.097(103)
1989		0.077(13)											0.077(13)
1990	0.150(30)					0.667(3)							0.197(33)
Georgia													
1986					0.032(31)	0.015(66)							0.021(97)
1988					0.105(19)	0.154(13)	0.118(5)						0.106(47)
1989				0.42(36)			0.100(90)		0.188(16)				0.102(142)
1990					0.035(43)	0.000(3)	0.197(60)						0.123(106)
South Carolina													
1985							0.048(31)*	0.013(78)					0.023(109)*
1986						0.000(19)	0.022(113)*						0.019(132)*
1988				0.111(9)	0.180(50)*	0.100(75)		0.231(130					0.139(147)*
1989				0.083(18)	0.237(17)	0.021(29)	0.056(45)						0.064(109)
1990					0.000(26)	0.060(29)							0.036(55)*
North Carolina and Virginia													
1985							0.000(17)		0.063(8)	0.047(95)	0.000(5)		0.040(125)
1986						0.023(132)							0.034(132)
1987					0.011(45)	0.060(50)	0.000(17)						0.031(112)
1988						0.188(8)	0.083(30)						0.105(38)
1989					0.024(21)	0.000(18)							0.013(39)

[1] *PEPA-2*a* allele frequencies by month. In parenthesis ( ) is number of fish. Asterisk (*) means sample phenotypic distribution deviated from Hardy-Weinberg expectations ($P<0.05$).
[2] Key West to Pensacola, FL. Months 1–4 from Ft. Meyers to Key West, FL. Months 5–12 from Panama City to Pensacola, FL.
[3] Texas (east) is Galveston, TX. Texas (south) is Port Aransas to Brownsville.

Results

Of the 50 loci surveyed in 1985, 30% were variable. In 1988, the 50 loci were again surveyed (879 fish from 10 locations) and 24% of the loci were found to have variants. Variations other than dipeptidase (EN 3.4.-.-) *PEPA-2** were found in low frequency (uncommon allele 0.000 to 0.063) in 18 polymorphic systems. Occurrence of these variants differed between locations and years. Electrophoretic variants were found for loci including aspartate aminotransferase (EN 2.6.1.1) *sAAT**, acid phosphatase (EN 3.1.3.2) *ACP-2**, adenosine deaminase (EN 3.5.4.4) *ADA**, adenylate kinase (EN 2.7.4.3) *AK-1** and *AK-2**, alanine aminotransferase (EN 2.6.1.2) *ALAT-1** and *ALAT-2**, esterase-D (EN 3.1.-.-) *ESTD-2** and *ESTD-3**, fructose-bis-phosphate aldolase (EN 4.1.2.13) *FBALD-2**, glucose-6–phosphate isomerase (EN 5.3.1.9) *GPI-1** and *GPI-2**, isocitrate dehydrogenase (NADP+) (EN 1.1.1.42) *sIDHP**, malic enzyme (NADP+) (EN 1.1.1.38) *ME-2**, mannose-6–phosphate isomerase (EN 5.3.1.8) *MPI**, dipeptidase (EN 3.4.-.-) *PEPA-1**, phosphogluconate dehydrogenase (EN 1.1.1.44) *PGDH**, and phosphoglucomutase (EN5.4.2.2) *PGM-2**.

Use of very low-frequency variations for stock identification of king mackerel was impractical, because sufficient sample sizes (numbers of fish) for detection during short time periods (one month or less) were unavailable. Tagging studies (Fable et al., 1990[4]) indicated that discrete geographic population units were not available during the time intervals required to obtain sufficient samples. Only dipeptidase (glycyl-leucine substrate)[5] consistently varied between locations. In 1985 (1,223 fish), 1986 (1,537 fish), 1987 (2,120 fish), 1988 (1,631 fish), 1989 (1,502 fish), and 1990 (963 fish), muscle tissues were examined for the dipeptidase variation. This enzyme developed on electropherograms as two zones of activity, and showed the pattern of a two allele (**a* and **b*) polymorphism in the most anodal zone (*PEPA-2**, in most collections, as described by May [1983]). We refer to May's 1 and 2 alleles (electromorphs) as **a* and **b*, respectively (Fig. 1). A third allele (**c*) which is anodal of the **a* allele was found in 1988 and 1989 collections from Veracruz, Mexico to Alabama.[6] Only one homozygote (**c***c*) and 20 heterozygotes (**c***a*) were found from 3,487 fish.

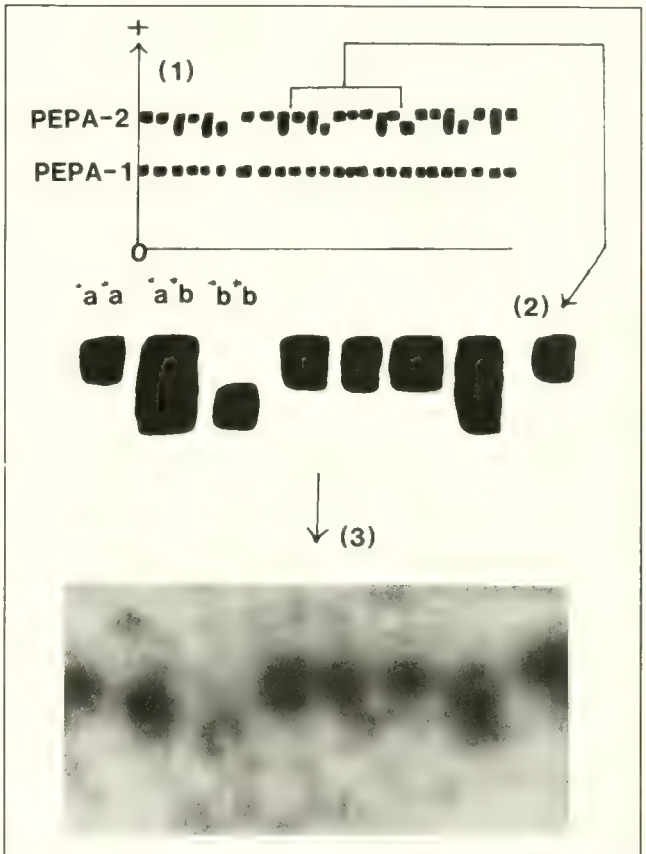

Figure 1

King mackerel (*Scomberomorus cavalla*) dipeptidase (*PEPA-1** and *PEPA-2**): (1) schematic of gel with 25 samples (*PEPA-2***a* is 0.700), (2) schematic of enlargement of section of *PEPA-2** on gel showing three phenotypes (**a***a*, **a***b*, **b***b*), and (3) photograph of actual gel section used for schematic (2).

Because of the rareness of this allele (**c*), it was combined with allele **a* for analysis.

Allele frequencies and phenotypic distributions varied extensively within and between areas from 1985 to 1990 (Table 1). The majority of monthly collections conformed to the Hardy-Weinberg expectation; however, many of the yearly collections did not conform. In general, higher **a* allele frequencies were found west of Florida than in Florida and along the Atlantic coast.

The phenotypic distributions of the dipeptidase polymorphism were not significantly correlated with body length, with few exceptions. When the phenotypic distribution was compared by 100–mm-FL size intervals for five geographic locations (Atlantic coast, Alabama-Mississippi, Louisiana, east Texas, and south Texas) by year, only seven of the 78 comparisons were significantly different (Kolmogorov-Smirnov goodness-of-fit test, $P<0.05$). Four of these

[5] Enzyme is also active with valyl-leucine and leucyl-tyrosine as substrates.

[6] The genetic nomenclature for this polymorphic system according to the recommendations of Shaklee, et al. (1990), is dipeptidase 3.4.-.-(*PEPA-2**) with three variant alleles **110*, **105*, and **100*. These alleles are represented in this report as **c*, **a*, and **b*, respectively.

deviant collections occurred in the northern Gulf (east Texas and Alabama-Mississippi). The other three (1988–*a*a* phenotype on Atlantic coast; 1989–*b*b*, and 1990–*a*a* phenotypes in northwest Florida) are believed to have resulted from sampling inadequacies (in 1988, only 9 *a*a were collected on the Atlantic coast, and in 1989 northwest Florida had 136 of the 275 *b*b in the <600–mm-FL cell, which represented 167 of the 344 fish; and in 1990, northwest Florida had 12 *a*a of the 17 *a*a in the 900, 1,000, and >1,100 mm cells).

When allele distributions were compared by sex at seven locations for each year in which sufficient data were available, eight of the 23 allele comparisons deviated significantly (chi-square contingency test, $P<0.05$). Six deviant collections occurred in the northern Gulf (Texas-Mississippi 1985–1989) and were from collections that did not conform to Hardy-Weinberg expectations with regard to their phenotypic distributions. Two others occurred in Veracruz, Mexico (1988 and 1990). The total allele-sex (1985–90) comparisons for the seven locations did not deviate significantly, except for Veracruz, Mexico. Veracruz collections were dominated by small fish (<600 mm FL) of which sex determination was difficult, especially early in the year (Jan.–July) because of undeveloped gonads. Sex could only be determined for 68% of the fish tested from this area.

The geographic pattern of dipeptidase (*PEPA-2**) (1985–90) indicated that western Gulf differed from eastern Gulf and Atlantic coast king mackerel. In all years except 1985, comparison of allele counts (Table 1) of the various geographic groupings of the Gulf varied significantly ($P<0.05$) both within the Gulf and between the Gulf and the Atlantic coast. On the Atlantic coast (north of Florida vs. Florida), the variation was found not significant (except in 1990). The trend in these comparisons was for excess *a allele in the western Gulf and for excess *b allele in the eastern Gulf and the Atlantic coast.

Discussion

Comparisons of subdivisions (Table 2) show a consistently higher level of *PEPA-2*a* in western Gulf king mackerel and a deficit of this allele in king mackerel in the eastern Gulf and along the Atlantic coast.

Electrophoretic data (ours and that of May (1983)[3] indicating high dipeptidase *PEPA-2*a* frequency in the western Gulf and low *a frequency in the eastern Gulf and along the Atlantic coast supports a two stock hypothesis for king mackerel in the Gulf. Supporting information can be obtained from other investigations: mark-recapture (Fable et al., 1990[4]), charterboat catches (Trent et al., 1987b) and spawning date analysis (Grimes et al., 1990). Fish movements indicated by mark-recapture are consistent with the two stock hypothesis. The charterboat information provides evidence of simultaneous northward migration on both sides of the Gulf, while the spawning date information offers evidence for reproductive isolation.

The king mackerel dipeptidase (*PEPA-2**) variation found in 1985–90 was similar to the variation first reported by May (1983)[3]. His data showed higher dipeptidase *a allele frequencies for Louisiana (0.618) and Texas (0.736) than were found eastward.

Temporal variations in the *PEPA-2** allele frequencies are difficult to interpret without taking into consideration the migratory behavior. The variation was extreme at some locations, giving the impression that the samples were collected from different or mixed schools from different origins. For example, in east Texas (Galveston-Freeport area) (1986), five discrete collections (5 July–28 August) of 27 to 56 fish each (204 total) were sampled. The *PEPA-2*a* frequencies were 0.933, 0.769, 0.202, 0.839, and 0.037 (in collection order). In other collection periods, variations in frequencies indicated that we had sampled the same school of fish. For example, in Louisiana (1987) three collections 7 days apart (21 Aug.–4 Sept.) were obtained. Their *PEPA-2*a* frequencies were 0.590 (50 fish), 0.580 (50 fish), and 0.594 (48 fish). In view of the extreme variability of *PEPA-2** frequencies, numerous deviations from Hardy-Weinberg expectations, and sampling difficulties (one or more schools per collection), proper spatial subdivision and grouping of collections for testing specific hypotheses is arduous. The expanse of the sampling area (Virginia to Yucatan) can be divided into various subdivisions representing distance or physical features (Table 2). Examples of subdivisions by distance are the following: Mississippi westward vs. Alabama eastward, Alabama to Florida Keys, Florida vs. Atlantic coast, and Florida east vs. Georgia northward. Examples of physical subdivisions are the following: Florida peninsula (Florida east coast versus Florida west coast), eastern Gulf and Atlantic coast (Alabama to Florida Keys versus Atlantic coast), and northern and western Gulf (Louisiana-Mississippi versus Texas versus Mexican sector of the Gulf) (See also Collard and Ogren, 1990).

Caution should be applied to interpreting electrophoretic results in which variation has not been proven to be of genetic origin by the use of breeding analysis (i.e., crossing of phenotypes and analy-

sis of offspring). Deviation from Hardy-Weinberg expectations can result from stock mixing, natural selection, or drift in small populations (Smith, 1990). While we favor the interpretation that these king mackerel data suggest stock mixing, consideration should be given to natural selection as the ultimate maintenance factor of *PEPA-2** frequencies as suggested for dipeptidase (*PEPA-LT**) and other variations found in *Menidia beryllina* (Johnson, 1974).

Electrophoretic data suggest that two stocks of king mackerel occur in the Gulf, a western stock with high frequency of the **a* allele and an eastern stock with a low frequency of the **a* allele. The northern Gulf appears to be a zone of mixing of these two stocks during the summer. Our electrophoretic information does not distinguish the eastern Gulf fish from those along the Atlantic coast.

Historical tagging data showed migration between south Florida and the north and northwest Gulf. Williams and Godcharles (1984)[2] (and Sutter et al.'s later analysis (1991) of Williams and Godcharles' data) can be examined in light of the two stock hypothesis. Williams and Godcharles tagged approximately 12,000 king mackerel off south and southeast Florida, primarily in winter months. Forty-nine tags were recovered in the northeast Gulf and another 49 tags were returned from the northwest Gulf. Almost all tagged fish were recaptured in the warmer months of the year, supporting the hypothesis of migration from wintering grounds in southeast Florida waters to northern Gulf of Mexico waters

Table 2

Comparisions of geographic groupings of allele counts of dipeptidase (*PEPA-2**) in king mackerel. (*Scomberomorus cavalla*), 1985–90.

Location[1]	Year	Alleles	χ^2	df	*P*	Remarks
MS westward vs. AL eastward (distance)[2]						
	1985	1,620	297.3417	1	<0.001	Deficient **b* in MS westward
	1986	1,676	340.9499	1	<0.001	Devidient **b* in MS westward
	1986	3,976	283.7311	1	<0.001	Deficient **b* in MS westward
	1988	2,468	812.6335	1	<0.001	Excess **b* east of Al Deficient **a* east of AL
	1990	1,926	793.5280	1	<0.001	Excess **b* east of AL Deficient **a* east of AL
Key West, FL westward vs. Atlantic coast (physical)						
	1985	2,630	329.0983	1	<0.001	Excess **a* in Gulf
	1986	2,662	879.2843	1	<0.001	Excess **a* in Gulf
	1987	3,865	271.3356	1	<0.001	Excess **a* in Gulf
	1988	3,084	643.4390	1	<0.001	Excess **b* in Atl. coast Deficient **a* in Gulf
	1989	3,004	657.913	1	<0.000	Excess **b* in Atl. Coast Deficient **a* in Atl. Coast
	1990	1,926	339.2062	1	<0.001	Excess **b* in Atl. coast Deficient **a* in Atl. coast
AL to Key West, FL vs. Atlantic coast (distance)						
	1985	1,518	0.0040	1	>0.90	
	1986	1,258	33.1770	1	<0.001	Excess **a* in Gulf
	1987	1,550	64.6325	1	<0.001	Deficient **a* in Atl. coast
	1988	1,022	10.4639	1	<0.001	Excess **a* in Atl. coast Deficient **a* in Gulf
	1989	1,406	6,2033	1	>0.01	Excess **a* in Gulf Deficient **a* in Atl. Coast
	1990	864	22.0855	1	<0.001	Excess **a* in AL to Key West, FL Deficient **a* in Atl. coast
Within northern and western Gulf (LA-MS, TX, MX) (physical)						
	1985	1,110	7.9835	2	>0.01	
	1986	1,410	135.5281	3	<0.001	Excess **b* in LA-MS Excess **a* in MX
	1987	2,416	71.5602	2	<0.001	Excess **b* in LA-MS Excess **a* in MX
	1988	2,062	40.1994	2	<0.001	Excess **b* in LA-MS Deficient **b* in TX
	1989	1,598	70.2421	2	<0.001	Excess **b* in LA-MS Deficient **a* in LA-MS
	1990	1,062	120.9159	2	<0.001	Excess **b* in LA-MS Deficient in **a* in LA-MS Deficient in **b* in MS
Within Atlantic coast (N of FL vs. FL) (distance)						
	1985	1,008	0.0738	1	>0.70	
	1986	992	1.8493	1	>0.10	
	1987	336	0.1133	1	>0.70	
	1988	616	0.9336	1	>0.30	
	1990	388	6.0278	1	>0.01	Excess **a* in FL

[1] Abbreviations are used for states: AL=Alabama; FL=Florida, LA=Louisiana, MS=Mississippi, TX=Texas, MX=Mexico

[2] In parentheses ( ) general classification of range subdivisions. See text

in the summer. These authors also tagged fish off North and South Carolina, but none were recovered in the Gulf.

According to Fable et al. (1990),[4] king mackerel tagged in northwest Florida have been recovered in south Florida. Typically, these are the smallest and youngest tagged in the southeast United States. Sutherland and Fable (1980) showed that northeast Gulf fish migrated to south Florida. However, additional tagging (Fable et al., 1990[4]) showed that northeast Gulf fish eventually moved westward to Louisiana, Texas, and Mexico waters when they had been free for a sufficient time and grown to a larger size.

Tagging off Louisiana from 1983 to 1985 (Fable et al., 1987) indicated that the northwest Gulf may have year round residental large king mackerel that mix in the warm months with smaller migrants from south Florida and Mexico. Recent tagging data (Fable et al., 1990[4]) from this region have provided additional recoveries from both south Florida and Mexico, strengthening this interpretation. Additional support is provided by the occurrence in Louisiana of a year-round king mackerel fishery, whereas elsewhere the fishery is seasonal.

In contrast to historical reports, recent tagging (Fable et al., 1990[4]) showed movements between Texas and Mexico. Fish tagged in Texas waters migrate to both Florida and Mexico. Additionally, fish movements between Texas and eastward (as far as Panama City, FL) were documented.

Mark-recapture data (Fable et al., 1990[4]) from tagging in Mexican waters suggest that the states of Campeche and Yucatan are wintering areas for king mackerel in the western Gulf. Fish tagged in warmer months (April–July) in Texas, Tamaulipas, and Veracruz were found in Campeche and Yucatan in the winter. Tagging efforts (Fable et al., 1990[4]) in Veracruz have provided evidence of northward migrations to Tamaulipas and Texas in spring and summer, and movement to the Yucatan peninsula in winter.

Additional evidence supporting two Gulf stocks can be found in catch-effort data of king mackerel. Although the data are complicated by different fishing strategies depending on the type of fishery (recreational or commercial) and regulatory closures, detailed analysis of catch data from the southeastern United States charterboat fishery indicated that in spring and early summer some stocks of fish simultaneously migrated northward along the western and eastern coasts of the Gulf (Trent et al., 1987b). They also developed the "... idea that part of the population of large fish remains in the Louisiana area year-round and that the abundance of these fish is greatest during cold months."

The fishery for king mackerel in Louisiana is unique among the fisheries in the northern Gulf of Mexico in that it is year-round; elsewhere it takes place mainly from late spring to late fall. The winter fishery (commercial hook-and-line) in Louisiana began in 1981–82. Distinctive differences characterized winter and spring-fall seasons: 1) the smallest fish (both males and females) were caught April to October whereas the largest fish were caught between November and March; 2) females were more abundant in the winter fishery than at other times of the year (Trent et al., 1987a).

For two or more populations to maintain separate identities they must be isolated, either physically or reproductively (Hartl, 1980). In the case of Gulf king mackerel, there is evidence for reproductive isolation. Grimes et al. (1990) presented a detailed examination of the distribution and occurrence of larval and juvenile king mackerel in the Gulf (based on published reports, neuston sampling, and Mexican trap net and trawl collections). The spawning season in the northern Gulf (U.S. waters), as indicated by the seasonal occurrence of larvae, is May to October. Larval collections off Mexico were sparse and offered little information on spawning seasonality.

The summer spawning period in the northern Gulf was also indicated by seasonal gonadal development of king mackerel (Finucane et al., 1986). They reported that reproductive activity occurred from May through September; a few fish were reproductively active as early as April and as late as October. However, spawning dates of January through August for Mexican juveniles estimated from otolith data showed a bimodal distribution, which suggests that spawning seasons in Mexican waters are different from those in the northern Gulf (Grimes et al., 1990).

Two of the four collections of juvenile king mackerel in Mexico used by Grimes et al. (1990) had tissue samples (Tampico, July 1986, and Playa Norte, Sept. 1986), and we analyzed these samples for *PEPA-2** variation. Spawning dates of fish in the Tampico collection ranged from mid-February to mid-April and *PEPA-2*a* frequency was 0.896. The Playa Norte collection's spawning dates ranged from mid-April to mid-July, and *PEPA-2*a* frequency was 0.600 (Table 1).

Water circulation data for the Gulf of Mexico (Salsman and Tolbert, 1963[7]) and information from Trent et al. (1987b), Grimes et al. (1990), Fable et al. 1990,[4] along with our data on king mackerel, sug-

[7] Salsman, G. G., and W. H. Tolbert. 1963. Surface currents in the northeastern Gulf of Mexico. U.S. Navy Mine Defense Laboratory, Panama City, FL, Res. and Dev. Rep. 209, 43 p.

gest one plausible scenario with regard to king mackerel stocks in the Gulf of Mexico. A western population exists that winters and spawns in the Gulf of Campeche. The Mexican Current serves as an entrainment system for its young. As these young become older and larger, they are able to cross the region of offshore advection and utilize the northern Gulf area (Texas to Florida) for summer feeding. This stock of fish has a high *PEPA-2*a* frequency and spawns earlier in the year than fish in the northern and eastern Gulf of Mexico. No information (tagging, electrophoretic, or reproductive) is available on fish of the Yucatan Straits area and the Caribbean Sea to evaluate their relation to the western Gulf of Mexico fish. An eastern population of king mackerel uses the eastern and northern Gulf of Mexico area as entrainment systems for its young and the northern Gulf (Florida-Texas) as summer feeding grounds. The spawning area extends from Texas to northwest Florida between April and October; the majority of spawning probably occurs in the northwest Florida-Louisiana area. Tagging studies suggest that this stock uses south Florida and the southeast coast of Florida as its wintering grounds.

The Louisiana area is somewhat of an enigma. Tagging studies indicate that the area is used by fish from both sides of the Gulf, fish are in the area yearround, *PEPA-2*a* frequencies are between the extremes of the east and west Gulf, and tag recoveries from winter tagging in Louisiana have been from Louisiana and westward, whereas recoveries from summer tagging were both east and west of Louisiana. Additionally, Finucane et al. (1986) suggested an earlier distinct peak in gonadal development (May) for Louisiana-Mississippi than in northwest Florida (August) and in Texas (August). The question still remains: Does the Louisiana area have an independent spawning population that utilizes the northern Gulf currents for its life cycle? The existing evidence (especially tagging) suggests the area is not independent; however, information comes from larger fish. Thus, the area may be occupied by individuals from both sides of the Gulf which may or may not reproduce in the area. Further investigation especially on the younger life stages using other methods of analyses may answer this question.

Another group (stock) of king mackerel that impinges upon the Gulf of Mexico resources (officially recognized by Fishery Management Councils) is the Atlantic Migratory Group. This group has a varying range from Virginia to southwest Florida depending on the time of the year (Gulf of Mexico and South Atlantic Fishery Management Councils, 1985). The stock is considered to winter in South Florida and ranges along the Atlantic coast to North Carolina and South Carolina during the summer. The fish probably spawn from May to October with a peak in July (Finucane et al., 1986). These fish are currently regulated as a group with seasonal southern boundaries of lat. 25°48'N (the Collier/Monroe County line, FL) from 1 April to 31 October and lat. 29° 25'N (the Volusia/Flagler County line, FL) from 1 November to 31 March. Tagging information supports this separation (Gulf of Mexico and South Atlantic Fishery Management Councils, 1985).

*PEPA-2*a* allele frequencies are generally low (0.00–0.10) along the Atlantic coast as in the eastern Gulf of Mexico. The higher *PEPA-2*a* values (>0.10) occasionally encountered may be the result of fish entrapped in water masses coming up the coast from outside the east coast of Florida. This possibility is suggested by the recovery along this coast of drift bottles that were released in the Yucatan Straits area (Salsman and Tolbert, 1963[7]).

All these stocks need to be further investigated in order to be elevated to the status of genetic stocks (i.e., completely isolated reproductive populations of the same species).

Conclusion

Four lines of evidence for a two stock hypothesis for the Gulf of Mexico king mackerel have been presented. The two stock hypothesis states that the Gulf contains a western stock of king mackerel, which winters in Mexico and migrates in spring and early summer to the northern Gulf (Texas-Alabama), and an eastern Gulf stock which winters in south Florida and migrates in spring and early summer to the northern Gulf. The two stocks mix in the northern Gulf during the summer.

The four lines of evidence are the following:

1 Dipeptidase (*PEPA-2**) data showing western Gulf fish high in **a* allele and eastern fish low in **a* allele.
2 Mark-recapture data showing movement along both sides of the Gulf from south to north.
3 Catch data indicating simultaneous migrations northward on each side of the Gulf in early spring and summer.
4 Estimates of spawning dates suggesting possible temporal and spatial differences between the northern and southern Gulf.

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Literature cited

Aebersold, P. B., G. A. Winans, D. J. Teel, G. B. Milner, and F. M. Utter.
1987. Manual for starch gel electrophoresis: a method for the detection of genetic variation. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 61, 19 p.

Baughman, J. L.
1941. Scombriformes, new, rare, or little known in Texas waters with notes on their natural history or distribution. Texas Acad. Sci. Trans. 24:14–26.

Clayton, J. W., and D. N. Tretiak.
1972. Amine-citrate buffers for pH control in starch gel electrophoresis. J. Fish. Res. Board Canada 29:1169–1172.

Collard, S. B., and L. H. Ogren.
1990. Dispersal scenarios for pelagic post-hatchling sea turtles. Bull. Mar. Sci. 47:233–243.

Collette, B. B., and E. C. Nauen.
1983. FAO species catalogue. Vol. 2: Scombrids of the world. An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. FAO Fish. Synop.125(2), 137 p.

Deuel, D. G.
1973. 1970 salt-water angling survey. U.S. Natl. Mar. Fish. Serv. Curr. Fish. Stat. No. 6200, 54 p.

Deuel, D. G., and J. R. Clark.
1968. The 1965 salt-water angling survey. U.S. Fish. Wildl. Serv., Resour. Publ. 67, 51 p.

Fable Jr., W. A., L. Trent, G. W. Bane, and S. W. Ellsworth.
1987. Movements of king mackerel, *Scomberomorus cavalla*, tagged in southeast Louisiana, 1983–85. Mar. Fish. Rev. 49(2):98–101.

Finucane, J. H., L. A. Collins, H. A. Brusher, and C. H. Saloman.
1986. Reproductive biology of king mackerel, *Scomberomorus cavalla*, from the southeastern United States. Fish. Bull. 84:841–850.

Grimes, C. B., A. G. Johnson, and W. A. Fable Jr.
1987. Delineation of king mackerel (*Scomberomorus cavalla*) groups along the U.S. east coast and in the Gulf of Mexico. *In* H. E. Kumpf, R. N. Vaught, C. B. Grimes, A. G. Johnson, and E. L. Nakamura (eds.), Proceedings of the stock identification workshop, p. 186–187. Dep. Commer., NOAA Tech. Memo. NMFS-SEFC-199.

Grimes, C. B., J. H. Finucane, L. A. Collins, and D. A. Devries.
1990. Young king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico, a summary of the distribution and occurrence of larvae and juveniles, and spawning dates for Mexican juveniles. Bull. Mar. Sci. 46:640–654.

Gulf of Mexico and South Atlantic Fishery Management Councils.
1985. Final amendment 1, fishery management plan and environmental impact statement for coastal migratory pelagic resources (mackerels) in the Gulf of Mexico and South Atlantic region, Tampa, FL, var. p.

Hartl, D. L.
1980. Principles of population genetics. Sinauer Assoc. Inc., Sunderland, MA, 488 p.

Johnson, M. S.
1974. Comparative geographic variation in *Menidia*. Evolution 28:607–618.

Kristjansson, F. K.
1963. Genetic control of two pre-albumins in pigs. Genetics 48:1059–1063.

Kutkuhn, J. H.
1981. Stock definition as a necessary basis for cooperative management of Great Lakes fish resources. Can. J. Fish. Aquat. Sci. 38:1476–1478.

Manooch III, C. S.
1979. Recreational and commercial fisheries for king mackerel, *Scomberomorus cavalla*, in the South Atlantic Bight and Gulf of Mexico, U.S.A. *In* E. L. Nakamura and H. R. Bullis Jr. (eds.), Proceedings of the mackerel colloquium, p. 33–41. Gulf States Mar. Fish. Comm., Rep. No. 4.

Manooch III, C. S., E. L. Nakamura, and A. B. Hall.
1978. Annotated bibliography of four Atlantic scombrids: *Scomberomorus brasiliensis*, *S. cavalla*, *S. maculatus*, and *S. regalis*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 418, 166 p.

Markert, C. L., and I. Faulhaber.
1965. Lactate dehydrogenase isozyme patterns of fish. J. Exp. Zool. 159:319–332.

Rivas, L. R.
1951. A preliminary review of the western north Atlantic fishes of the family Scombridae. Bull. Mar. Sci. Gulf Caribb. 1(3):209–230.

Royce, W. F.
1972. Introduction to the practice of fishery science. Acad. Press, New York, 428 p.

Shaklee, J. B., F. W. Allendorf, D. C. Morizot, and G. S. Whitt.
1990. Genetic nomenclature for protein-coding loci in fish. Trans. Am. Fish. Soc. 119:2–15.

Smith, P. J.
1990. Protein electrophoresis for identification of Australasian fish stocks. Aust. J. Mar. Freshwater Res. 41:823–833.

Sokal, R. R., and F. J. Rohlf.
1981. Biometry. W. H. Freeman and Co., New York, NY, 859 p.

Sutherland, D. F., and W. A. Fable Jr.
1980. Results of a king mackerel (*Scomberomorus cavalla*) and Atlantic Spanish mackerel (*Scomberomorus maculatus*) migration study, 1975–79. U.S. Dep. Commer., NOAA Tech. Memo., NMFS-SEFC-12, 18 p.

Sutter III, F. C., R. O. Williams, and M. F. Godcharles.
1991. Movement patterns and stock affinities of king mackerel in the southeastern United States. Fish. Bull. 89:315–324.

Swofford, D. L., and R. B. Selander.
1981. Biosys-1. A computer program for the analysis of allelic variation in genetics. Release 1. University of Illinois at Urbana, Champaign, IL, 66 p.

Trent, L., W. A. Fable Jr., S. J. Russell, G. W. Bane, and B. J. Palko.
1987a. Variation in size and sex ratio of king mackerel, *Scomberomorus cavalla*, off Louisiana, 1977–85. Mar. Fish. Rev. 49(2):91–97.

Trent, L., B. J. Palko, M. L. Williams, and H. A. Brusher.
1987b. Abundance of king mackerel, *Scomberomorus cavalla*, in the southeastern United States based on CPUE data from charterboats 1982–85. Mar. Fish. Rev. 49(2):78–90.

U.S. Department of Commerce.
1984. Fisheries of the United States, 1983. NOAA, NMFS, Curr. Fish. Stats. No.8320, 121 p.

1986. Marine recreational fishery statistics survey, Atlantic and Gulf coasts, 1985. NOAA, NMFS, Curr. Fish. Stats. No. 8327, 130 p.

1987. Fisheries of the United States, 1986. NOAA, NMFS, Curr. Fish. Stats. No.8385, 119 p.

Reproductive biology and egg production of three species of Clupeidae from Kiribati, tropical central Pacific

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Abstract.—The spawning seasonality, fecundity, and daily egg production of three species of short-lived clupeids, the sardine *Amblygaster sirm*, the herring *Herklotsichthys quadrimaculatus*, and the sprat *Spratelloides delicatulus* were examined in Kiribati to assess whether variable recruitment was related to egg production. All species were multiple spawners, reproducing throughout the year. Periods of increased spawning activity were not related to seasonal changes in the physical environment. Spawning activity and fish fecundity were related to available energy reserves and, hence, food supply. The batch fecundity of *A. sirm* and *S. delicatulus* also varied inversely with hydrated oocyte weight.

The maximum reproductive life span of each species was less than nine months and averaged two to three months. Each species had a similar spawning frequency of three to five days, but this varied more in *A. sirm* and *S. delicatulus*. *Amblygaster sirm* had the highest fecundity and potential lifetime egg production, but the number of eggs produced per kilogram of fish was highest in the small sprat *S. delicatulus*.

Monthly estimates of the daily egg production of each species varied with the proportion of the population that was spawning. Estimates of egg production showed little similarity to the frequency distribution of birthdates back-calculated from length-frequency samples. The distribution of back-calculated birthdates confirmed that fish spawned in all months, but the proportion born each month varied widely from species to species and year to year. The reproductive strategy of these species ensures that successful spawning is likely, and so the level of recruitment is more dependent on post-hatching survival rates than on egg production.

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The sprat *Spratelloides delicatulus*, the herring *Herklotsichthys quadrimaculatus*, and the sardine *Amblygaster sirm* are the dominant tuna baitfish species in the Republic of Kiribati (Rawlinson et al., 1992). All three species inhabit coral reef lagoons and adjacent waters. Sprats school in shallow water around reefs and adjacent seagrass during the day. Herring also form dense schools in shallow water along the shoreline and among reefs during the day (Williams and Clarke, 1983). Unlike the other species, sardines school near the bottom of the lagoon during the day (Conand, 1988). All species disperse into the mid and upper waters of the lagoon during the night to feed and become available to the commercial fishery.

A major source of lost fishing time by pole-and-line vessels in Kiribati has been irregular baitfish catches (MacInnes, 1990). These important tuna baitfish species have shown large seasonal and interannual fluctuations in abundance since they were first recorded during the 1940's (McCarthy, 1985[1]; Rawlinson et al., 1992). Both *A. sirm* and *H. quadrimaculatus* disappear from baitfish catches for variable periods and can be absent for months or years (Kiribati Fisheries Division, 1989[2]).

Changes in abundance may be related to variable or irregular recruitment, because many clupeoids (especially clupeids and engraulids) have little capacity to compensate for environmental variation during the period of peak spawning and egg production (Cushing, 1967, 1971).

Most clupeids, including some tropical species, are multiple spawners (Alheit, 1989). Multiple spawning should be advantageous for short-lived species because it enables them to maintain relatively stable population sizes in unpredictable environments (Armstrong and Shelton, 1990). Multiple spawning has been established for few tropical clupeids (e.g., *Sardinella brasiliensis*; Isaac-Nahum et al., 1988). Of the three major baitfish species in Kiribati, only *S. delicatulus* has been shown to be a multiple-spawner (Milton and Blaber, 1991). All three species are subject to high natural mortality in Kiribati (Rawlinson et al., 1992), thus lifetime egg production

[1] McCarthy, D. 1985. Fishery dynamics and biology of the major wild baitfish species particulary *Spratelloides delicatulus*, from Tarawa, Kiribati. Kiribati Fisheries Div., Tarawa, Kiribati, 53 p.

[2] Kiribati Fisheries Division. 1989. Fisheries Division 1989 Annual Rep., Ministry of Natural Resources Development, Tarawa, Kiribati, 38 p.

may be increased if they spawned multiple batches of eggs.

Egg production of multiple spawning species depends on reproductive life span, the time between spawnings, and the age structure of the population (Parrish et al., 1986). Batch fecundity of *S. delicatulus* varies widely between sites, both within and between countries (Milton et al., 1990). In a short-lived species such as *S. delicatulus* (<5 months; Milton et al., 1991), reproductive life span may have an important influence on potential lifetime egg production.

Batch fecundity of *H. quadrimaculatus* does not appear to vary throughout its distribution, and ranges from 4,000 to 10,000 eggs (Marichamy, 1971; Hida and Uchiyama, 1977; Williams and Clarke, 1983; Moussac and Poupon, 1986; Conand, 1988). Fish mature at about 90 mm in length at six months of age (Williams and Clarke, 1983), and they survive for at least one year (Milton et al., 1993). Little is known of fecundity and egg production of *A. sirm*. Fecundity of the species is related to length and weight, with a mean of 20,000 eggs per batch, and individuals probably spawn more than one batch of eggs (Conand, 1988).

Temperate clupeids vary widely in life-history parameters (e.g., *Clupea* spp., Jennings and Beverton, 1991). Food availability and environmental conditions affect the size and number of eggs of Pacific herring (*Clupea pallasi*) (Hay and Brett, 1988). Results of studies of temperate clupeoids suggest that they do not spawn during periods of high food abundance, but store energy as fat for later reproductive activity (Hunter and Leong, 1981; Iles, 1984). There are no similar studies of tropical clupeids. *Encrasicholina heterolobus*, a tropical engraulid, does not deplete energy reserves in the liver or soma during spawning (Wright, 1990). Fish with higher condition factor (*K*) also had higher fecundity.

Stored energy or fish condition that may influence both spawning frequency and batch fecundity have a marked influence on egg production and, hence, affect subsequent recruitment (Ricker, 1954; Beverton and Holt, 1957). Adult reproductive variation should strongly influence recruitment in short-lived tropical species that have short larval phases and rapid growth. An example is *S. delicatulus* which, in the Solomon Islands, live a maximum of five months and mature at about two months of age (Milton and Blaber, 1991; Milton et al., 1991). *Amblygaster sirm* and *H. quadrimaculatus* live less than two years (Milton et al., 1993) and mature in 6–12 months (Williams and Clarke, 1983; Conand, 1988).

In this study, we examined the variability in reproductive biology of the three major baitfishes in Kiribati to determine the influence of adult reproductive variability on subsequent recruitment. Our objective was to test the hypothesis that reproductive biology of short-lived clupeids is adapted to maintaining relatively stable population sizes. We determined potential life-time egg production and whether estimated egg production is related to the frequency distribution of back-calculated birthdates.

Methods and materials

Study areas

The Republic of Kiribati covers an area of 3×10^6 km^2 in the central Pacific ocean and comprises three main island groups (Gilbert, Phoenix, and Line Islands) (see Inset Fig. 1). The Gilbert Island group is the most populated, consisting of 16 coral reef islands. All islands in the group have a typical ocean platform coral reef structure and have been built up by scleractinian corals and coralline algae on a submerged mountain (Gilmour and Colman, 1990[3]). Most atolls consist of small islets lying on the eastern side of a lagoon with an open western side due to the prevailing easterly winds. Most typically have passages between the islets through which water is exchanged.

The four study sites (Abaiang, Butaritari, Tarawa, and Abemema) were typical of islands in the Gilbert Island group; all had narrow islets on their southern and eastern sides, except Abaiang (Fig. 1). Lagoons were mainly shallow (20–30 m deep), often with large areas of intertidal seagrass or sand on their eastern sides. Bottom topography of the deeper parts of the lagoon was generally smooth, with some coral outcrops. Our study sites were similar to those described by Hobson and Chess (1978) in the Marshall Islands.

Environmental parameters

On each sampling occasion, we measured the time of collection, sea surface temperature (°C), cloud cover (okters), wind direction and speed, and moon phase because these factors may be related to spawning or recruitment (Dalzell, 1985, 1987; Peterman and Bradford, 1987; Milton and Blaber, 1991). For each site, monthly rainfall data for 1989

[3] Gilmour, A. J., and R. Colman. 1990. Report on a consultancy on a pilot environmental study of the outer island development program, Republic of Kiribati. Graduate School of the Environment, Macquarie Univ., Australia, 151 p.

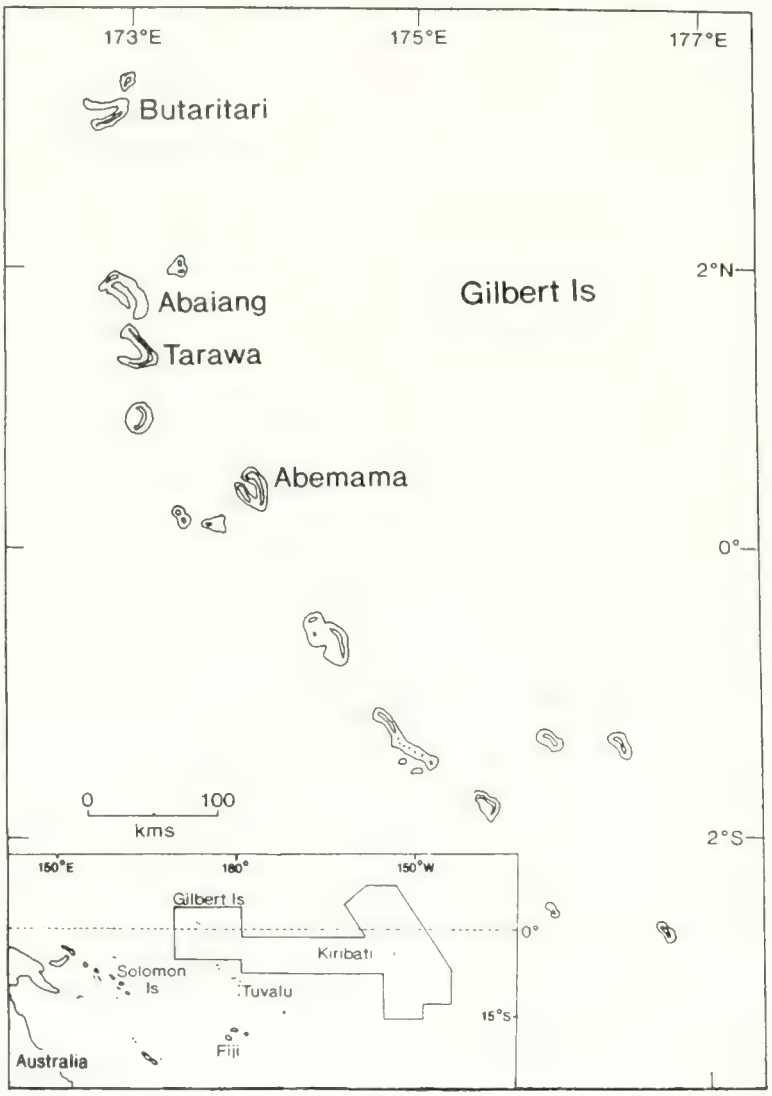

Figure 1

Map of Gilbert Islands, Kiribati showing the four study sites (Butaritari, Abaiang, Tarawa, and Abemama). Inset shows the territorial boundary of Kiribati, the Gilbert Islands, and their position in the Pacific.

and 1990 were obtained from the Kiribati Government Meteorological Division.

Sampling

Fifty to 1,000 *Amblygaster sirm*, *Herklotsichthys quadrimaculatus*, and *Spratelloides delicatulus* were collected monthly at one or more of four sites in Kiribati (Butaritari, Abaiang, Tarawa, and Abemama; Fig. 1) between August 1989 and May 1991. Additional samples of *A. sirm* and *H. quadrimaculatus* were collected in November 1988 and January 1989 from Tarawa. Fish were caught by several methods at each site. Most samples were collected from the commercial tuna baitfish catches each month at each site. Supplementary samples were obtained by beach-seining (*H. quadrimaculatus* and *S. delicatulus*), cast-netting (*H. quadrimaculatus*) in shallow water during the day, or gillnetting (25– and 38–mm stretched mesh) at night near baitfishing operations. All fish were preserved in 70% ethanol.

Reproductive biology

Laboratory studies All fish collected from commercial baitfish sampling were measured (standard length in millimetres), and a subsample of 20 to 60 specimens weighed (±0.005 g). Gonads, otoliths, liver, and viscera were removed and the amount of visible fat subjectively estimated. Both ovaries from the first 20 females of each species at each site for each month were dried of surface moisture, weighed (±0.001 g) and stored in 4% formalin-seawater for histology. Testes, ovaries of other fish, liver, and the soma were dried at 60°C to a constant weight. Otoliths were used to estimate the age (in days) of each fish by methods outlined in Milton et al. (1993). Additional samples of fish caught by other methods were treated separately, but in a similar way. We report only on results of studies of fish collected from commercial samples unless otherwise stated.

For histological preparations, gonads were embedded in paraffin, sectioned at 9 mm, and stained with Ehrlich's haemotoxylin and eosin (McManus and Mowry, 1964). Gonad maturation stages were defined following Cyrus and Blaber (1984) and Hunter and Goldberg (1980), and were similar to those of Moussac and Poupon (1986) for *H. quadrimaculatus* from the Seychelles. We staged each gonad according to the relative numbers of cells at each developmental stage (Young et al., 1987; Table 1), and the presence of any post-ovulatory follicles was noted. The percentage of each histological section that corresponded to each developmental stage was subjec-

Table 1

Criteria used for staging female gonads of tropical clupeids stained with haematoxylin and eosin.

Stage		Histology
(1)	Immature	Chromatin nucleolar stage — prefollicle cells surround each oocyte
(2)	Developing/resting	Perinucleolar stage — uniform staining cytoplasm
(3)	Maturing	Yolk vesicle formation; some non-staining yolk (lipid)
(4)	Ripe	Vitellogenic stage — red-staining yolk; developed chorion
(5)	Running ripe (spawning)	Globular red-staining yolk; oocytes hydrated; development complete
(6)	Spent	Presence of post-ovulatory follicles; cortical alveoli present and/or atresian of remaining ripe oocytes

tively estimated. Post-ovulatory follicles were aged according to stages found in other multiple-spawning clupeoids (Hunter and Goldberg, 1980; Goldberg et al., 1984; Isaac-Nahum et al., 1988). Gonosomatic indices (GSI) were calculated as the ratio of wet gonad weight to somatic weight (total weight minus gonad weight), expressed as a percentage. Similarly, we calculated a hepatosomatic index (HSI) as the ratio of liver dry weight to somatic dry weight (total weight minus entire viscera), expressed as a percentage.

Length and age at sexual maturity were defined as the minimum size and age at which fish had ripe oocytes (Stage 4), determined by histological examination. Fish that had running-ripe oocytes (Stage 5) were recorded as in spawning condition. We defined the length and age at first spawning as the smallest size where the proportion of running-ripe oocytes in the section exceeded 85% for more than 50% of the fish of that length or age. We chose this criterion after examining large numbers of histological sections with running-ripe oocytes. In these sections they always represented more than 85% of the section area. Our results were similar to that found in other tropical clupeoids (Milton and Blaber, 1991). The reproductive life span of the population of each species at each site each month was determined from the oldest fish (Milton et al., 1993) in each sample minus the age at first spawning.

We estimated batch fecundity for each species from fish that had been examined histologically and had oocytes that were starting to hydrate (ripe-early running ripe; Stages 4–5; Table 1), but we did not examine the fecundity of fish with any empty follicles. An advanced modal size group of oocytes could be distinguished in ripe fish. We separated a subsample of between half (*A. sirm*) and all (*S. delicatulus*) of the ovary and weighed it. The number of eggs in the advanced mode was counted and the fecundity was estimated by multiplying the number of eggs in the subsample by the ratio of total gonad weight to subsample weight. Fecundity estimates were made within three to four days after the ovary was removed from the fish to minimize the potential bias of differential absorption of fixative by oocytes and surrounding somatic tissue.

We used hydrated oocytes from fish caught between 2000 and 2330 hours to estimate egg weight. Oocyte weights were estimated from hydrated oocytes in ovaries that were almost ready to spawn (late Stage 5; Table 1). We measured oocyte dry weight by counting 10 samples of 10 oocytes from each ovary, drying the oocytes at 50° C to a constant mass and weighing each subsample separately.

We scored visceral fat on a five-point scale. If a fish had less than 25% of the intestine covered in fat deposits, it was scored as (1); 25–50%, (2); 50–75%, (3); and 75–100%, (4). A fish scored (5) when all intestine was covered with fat and deposits were also present around the stomach (Nikolsky, 1963).

The proportion of females examined histologically each month that had post-ovulatory follicles (POF; Stage 6) was used to evaluate reproductive seasonality. We determined that these fish had spawned within the previous 15–48 hours, because these structures decompose and cannot be recognised after that time (Hunter and Goldberg, 1980; Clarke, 1989). In samples where no fish had POF's, we used the proportion of fish in the histological subsample whose sections had greater than 85% running-ripe oocytes (Milton and Blaber, 1991). We used this proportion to calculate monthly estimates of mean daily oocyte production and the number of batches of oocytes spawned each month (Parrish et al., 1986).

We estimated daily oocyte production (n/kg of adults; egg production index) for samples collected from commercial baitfishing, because these samples were assumed to be most representative of the population. Our methods were similar to those of Parker (1980, 1985), which have been used to estimate the spawning biomass of a number of multiple spawners (Armstrong et al., 1988; Pauly and Palomeres, 1989; Somerton, 1990). However, our methods differed because we used commercial catch per unit of effort (CPUE) as an index of adult abundance.

$$\text{Egg production index} = \left(\sum (f_i p F_i S R_i) \Big/ \sum W_i\right) * CPUE \quad (1)$$

where f_i is the proportion of females in the ith length class, p is the proportion of the sample spawning, F_i is the fecundity of a fish of that length taken from the fecundity-length regression, SR_i is the sex-ratio of the ith length class and W_i is the total weight of fish in the ith sample. CPUE was estimated from the monthly catch returns of the commercial fleet. We chose this method of estimating egg production because *S. delicatulus* have demersal eggs (Leis and Trnski, 1989) and the eggs of *A. sirm* and *H. quadrimaculatus* are difficult to sample adequately in the large areas of suitable habitat in each lagoon.

For comparison with adult spawning data, we back-calculated the distribution of birthdates of fish collected in each length-frequency sample by using the growth equations of Milton et al. (1993). Frequencies in each age class were adjusted for mortality by using the estimates of Rawlinson et al. (1992). The distribution of birthdates was also back-calculated for *H. quadrimaculatus* and *S. delicatulus* length-frequency samples from previous studies at one site (Tarawa) January 1976 to February 1977 (R. Cross, 1978[4]) and May 1983 to April 1984 (McCarthy, 1985[1]). We used age distribution in these earlier studies and those of the present study to examine seasonal, annual, and site-related differences in the reproductive life span of each species.

Statistical analyses Inter- and intra-specific differences in fat index, HSI and K were examined with Fisher's t-tests to account for unequal sample sizes. Seasonal and site-related differences in fecundity (expressed as oocytes per gram) were examined by analysis of covariance with weight as the covariate. Hydrated oocyte weight and reproductive life span were examined by one-way analysis of variance.

We examined the relative influence of exogenous and endogenous factors on the fecundity of each species at each site by stepwise regression (Sokal and Rohlf, 1981). We included the following: length, weight, age, sea-surface temperature (°C), wind speed (in knots), moon phase (expressed by fitting a sin/cosin curve to the number of days since the last full moon before the sample was taken divided by the number of days in a lunar month (29.5) (Milton and Blaber, 1991), fish condition (K: weight/length^3), fat, and HSI(%). We retained only those variables that significantly improved the fit of the model ($P<0.05$). Because several of these variables were correlated, we did a partial-correlation analysis between these variables and fecundity, and the results of the two approaches were compared. If the variable most related to fecundity in the stepwise regression was not the one most related to fecundity in the partial-correlation analysis, the stepwise regression model was discarded and no relationship was assumed.

In order to estimate egg production (Eq. 1), we estimated the proportion of females in each 5-mm length class from the total sample of each species. The variance of these estimates was calculated by using the normal approximation to the binomial distribution (Walpole, 1974). We assessed whether the monthly percentage of annual egg production was related to the proportion of annual recruitment in the same month by rank-correlations (Conover, 1980).

The average age of the potential spawning population in each sample was compared by a nested analysis of variance with month of sampling nested within year. Significant differences between treatments were identified from comparison of the least-squares means of each treatment, as sample sizes differed between cells (Sokal and Rohlf, 1981).

Results

Environmental parameters

Sea-surface temperature in Kiribati varied little throughout the year. During the study period, temperatures varied between 29°C and 32°C (Table 2). Rainfall varied along the Gilbert Island group; rainfall was higher in Butaritari than at the other sites. Some rain fell throughout the study period but was more intense during 1990 at all sites. Rainfall during 1989 was below the long-term average at all sites and was 16–50% that of 1990. The highest rainfall fell during the north-east monsoon (December–April) at all sites. Winds were mostly light, and varied in direction seasonally, blowing from the east during the monsoon, but from the south-south-west for the rest of the year (Table 2).

Reproductive biology

Maturation The length and age at first maturity of *A. sirm* varied between sites (Table 3). *Amblygaster sirm* matured younger and smaller in Kiribati than elsewhere. Length and age at first spawning were much greater than the length or age when fish reached sexual maturity, but this size was similar to that of fish from northern Australia (Table 3). *Herklotsichthys quadrimaculatus* matured and were capable of spawning at 70 mm length and 4 months of age (Table 3). The relative size and age at which fish matured (as a proportion of maximum size and

[4] Cross, R. 1978. Fisheries research notes. Fisheries Division, Ministry of Commerce and Inductry, Tarawa, Kiribati, 58 p.

age) did not differ among fish from the four sites. In Kiribati, *S. delicatulus* become sexually mature at 40 mm and two months of age and spawn shortly afterwards. Compared to the other species, the length and age at maturity and first spawning varied less among sites (Table 3). The three species differed in the length and age at sexual maturity and first spawning. However, as a proportion of their maxima, the three species were similiar (*t*-test; $P>0.1$). All matured and spawned at about 70% of maximum size and 50% of maximum age (Table 3).

Table 2

Mean water temperature (°C), wind speed (kn), cloud cover, and monthly rainfall (mm) at four sites in Kiribati from November 1988 to May 1991.

Parameter	Butaritari	Abaiang	Tarawa	Abemama
Water temperature (°C)	30.2 ± 0.3	30.2 ± 0.4	29.5 ± 0.1	29.9 ± 0.2
Range	28–32	27–33	29–30	29–31
Wind speed (kn)	2.2 ± 0.6	4.2 ± 0.9	5.4 ± 1.2	2.2 ± 0.2
Range	0–7	0–10	1–15	1–5
Prevailing direction	East	East	East	East
Cloud cover (okters)	2 ± 0.6	5 ± 0.6	3 ± 0.5	1 ± 0.4
Range	0–6	1–7	0–7	0–4
Monthly rainfall (mm) (1945–88)	263 ± 35	181 ± 35	165 ± 35	128 ± 33
Range	7–908	0–761	0–824	0–728
Monthly rainfall 1989 (mm)	184 ± 29	42 ± 10	77 ± 23	36 ± 10
Range	51–351	0–108	6–235	3–102
Monthly rainfall 1990 (mm)	404 ± 37	–	298 ± 51	202 ± 31
Range	195–614	–	19–643	93–402
Months sampled	14	12	18	13

Timing of spawning We identified recent spawning by the presence of post-ovulatory follicles in the ovaries. In *A. sirm*, follicles were detected in samples collected between 0100 to 1630 hours, and new post-ovulatory follicles (identified as day-0 [<24 hr]; Hunter and Goldberg, 1980; Goldberg et al., 1984) were observed in fish collected between 0100 and 0510 hours. Female *H. quadrimaculatus* with post-ovulatory follicles were collected between 2130 and 1630 hours and day-0 follicles were found in samples collected between 2130 to 0300 hours. In female *H. quadrimaculatus* caught after 0300 hours, follicles could not be distinguished from day-1 type POF's, as the follicles degenerated rapidly. Similarly, we detected post-ovulatory follicles in female *S. delicatulus* collected from 2210 to 1930 hours, and follicles of all females collected earlier than 0845 hours were identified as day-0. Those in females of the single sample collected later in the day (1930) were assigned as day-1.

Spawning season There was protracted spawning in *A. sirm* with periods of intense spawning activity (Fig. 2). During both 1989 and 1990, fish spawned August to October and also during May-June in 1990. Condition, fat index, and HSI were less during spawning periods and reached a peak in March–April 1990, i.e., before spawning (Fig. 2). We found less fat deposits in spent fish and the fish were in poorer condition than fish with gonads in other stages of development ($P<0.05$; Table 4). We noted no significant differences in HSI among fish with gonads at the same stage of development.

Herklotsichthys quadrimaculatus spawned throughout the study period: 20 to 50% of the population spawned each month (Fig. 3). Female condition, fat index, and HSI all followed a similar pattern during the study but did not appear to be directly related to spawning activity. Fish in spawning condition had the highest HSI, fat, and condition values, but these were only significantly greater than those of spent fish ($P<0.05$; Table 4).

Spratelloides delicatulus spawned almost continuously throughout the study period but spawning varied in intensity (Fig. 4). Peak spawning occurred during different periods in each of the years sampled. Female HSI and fat index showed a similar pattern during the study but monthly changes in these parameters or fish condition did not follow the spawning cycle. We found no significant differences in HSI or fat index for females with ovaries in different stages of development ($P>0.1$; Table 4). Fish condition was lower among spent fish than in ripe or spawning fish ($P<0.05$; Table 4). Females with ripe ovaries had higher mean HSI, fat, and condition than those in other stages of development, but these differences were not significant (Table 4).

Fecundity The relative fecundity of *A. sirm* and *H. quadrimaculatus* did not differ among sites or seasonally within sites in Kiribati (ANCOVA with weight as covariate; overall $P>0.07$; Table 5). However, the relative fecundity of *H. quadrimaculatus* was significantly different between fish from Tarawa and Abemama (*t*-test; $P<0.05$). Batch fecundity of both species did not differ among sites in Kiribati. Within their respective species groups, both species had similar batch fecundities to the other species listed, although their relative fecundities were lower (Table 5).

Table 3

Length and age at sexual maturity and first spawning of *Amblygaster sirm*, *Herklotsichthys quadrimaculatus*, and *Spratelloides delicatulus* from various populations throughout their range. (L_{mat} = length at maturity, L_{fsp} = length at first spawning, L_{max} = maximum size, T_{mat} = age at maturity, T_{fsp} = age at first spawning, T_{max} = maximum age, K = Kiribati, I = India, SI = Solomon Islands).

Species	Site	Length at maturity (mm) (L_{mat}/L_{max})	Length at first spawning (mm) (L_{fsp}/L_{max})	Age at maturity(d) (T_{mat}/T_{max})	Age at first spawning (d) (T_{fsp}/T_{max})	Source[1]
A. sirm	Kiribati	110 (0.50)	180 (0.80)	150 (0.29)	330 (0.65)	(1)
	New Caledonia	132 (0.72)	—	295 (0.40)	—	(2)
	N. Australia	174 (0.79)	193 (0.88)	—	—	(3)
	Sri Lanka	166 (0.88)	—	~330 (0.80)	—	(4)
Mean		146 (0.72)	—	—		
H. quadrimaculatus	Hawaii	80 (0.63)	90 (0.70)	160 (0.53)	190 (0.63)	(5)
	Marshall Is.	90 (0.82)	—	190 (0.72)	—	(6)
	Fiji	95 (0.78)	98 (0.80)	275 (—)	294 (—)	(7), (8)
	Butaritari (K)	65 (0.68)	70 (0.74)	125 (0.50)	135 (0.53)	(1)
	Abaiang (K)	70 (0.74)	70 (0.74)	125 (0.37)	125 (0.37)	(1)
	Tarawa (K)	69 (0.72)	70 (0.73)	138 (0.45)	150 (0.48)	(1)
	Abemama (K)	70 (0.64)	72 (0.65)	140 (0.34)	150 (0.36)	(1)
	New Caledonia	91 (0.64)	—	244 (—)	—	(9)
	Andaman Is. (I)	99 (0.81)	104 (0.85)	—	—	(10)
	Seychelles	97 (0.71)	—	150 (0.30)	—	(11)
Mean		83 (0.72)	82 (0.74)	172 (0.46)	174 (0.47)	
S. delicatulus	Fiji	35 (0.56)	39 (0.63)	52 (0.43)	61 (0.51)	(7), (8)
	Butaritari (K)	40 (0.68)	40 (0.68)	65 (0.51)	68 (0.54)	(1)
	Abaiang (K)	45 (0.75)	53 (0.88)	62 (0.51)	80 (0.64)	(1)
	Tarawa (K)	45 (0.68)	50 (0.76)	77 (0.50)	90 (0.57)	(1)
	Munda (SI)	37 (0.58)	37 (0.58)	72 (0.47)	78 (0.51)	(12), (13)
	Vona Vona (SI)	37 (0.66)	37 (0.66)	68 (0.53)	72 (0.56)	(12), (13)
	Tulagi (SI)	38 (0.60)	38 (0.60)	73 (0.55)	75 (0.57)	(12), (13)
	Maldives	38 (0.69)	40 (0.73)	90 (0.60)	97 (0.65)	(13), (14)
	India	42 (0.71)	—	—	—	(15)
Mean		40 (0.66)	42 (0.69)	70 (0.51)	78 (0.57)	

[1] Sources: (1) present study, (2) Conand (1991), (3) Okera (1982), (4) Dayaratne and Gjosaeter (1986), (5) Williams and Clarke (1983), (6) Hida and Uchiyama (1977), (7) Lewis et al. (1983), (8) Dalzell et al. (1987), (9) Conand (1988), (10) Marichamy (1971), (11) Moussac anf Poupon (1986), (12) Milton and Blaber (1991), (13) Milton et al. (1991), (14) Milton et al. (1990), (15) Mohan and Kunhikoya (1986).

Using stepwise linear regression, we found that fecundity was related to weight in all species (Table 6; Fig. 5). Fecundity of *A. sirm* was significantly correlated with HSI and fish condition. Fish condition, HSI, and fat index were all correlated with fecundity in *H. quadrimaculatus* (Table 6). Fecundity was significantly correlated with weight and condition at two of the four sites. Although, when data from all sites were combined, weight and fat index were the only significant correlates.

Fecundity of *S. delicatulus* varied widely among sites, both within Kiribati and among countries (Table 5). In Kiribati, relative fecundity was higher at Butaritari than at Abaiang ($P<0.05$), but differed less than among sites in the Solomon Islands. Fecundity did not vary seasonally at any site. Relative fecundity of *S. delicatulus* was highest in New Caledonia — significantly higher than at all other sites except Butaritari in Kiribati (Table 5). However, the relative fecundity of *S. delicatulus* was lower than its congeners, *S. gracilis* and *S. lewisi*, at sites where they co-occurred (Table 5).

We found that the fecundity of *S. delicatulus* correlated strongly with fish weight (Fig. 5). The only other factor related to fecundity in *S. delicatulus* was HSI. There was a significant relationship between fecundity and HSI at Butaritari and Tarawa and when all data were combined. Spawning fish had a higher HSI at Butaritari than at other sites (2.24 ± 0.13 vs. 1.41 ± 0.08; $P<0.001$).

The HSI of male *S. delicatulus* that had a GSI similar to that of spawning females (>5%) was also

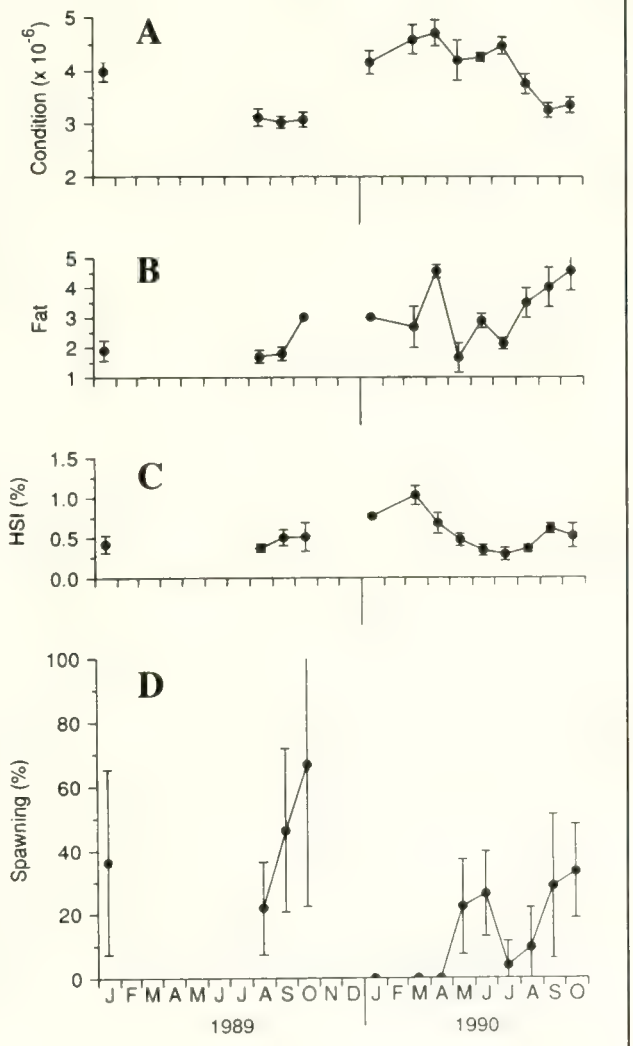

Figure 2

Monthly variation (±95% confidence limits) in (**A**) condition, (**B**) visceral fat index, (**C**) hepatosomatic index and (**D**) proportion spawning of female *Amblygaster sirm* from Kiribati between January 1989 and October 1990.

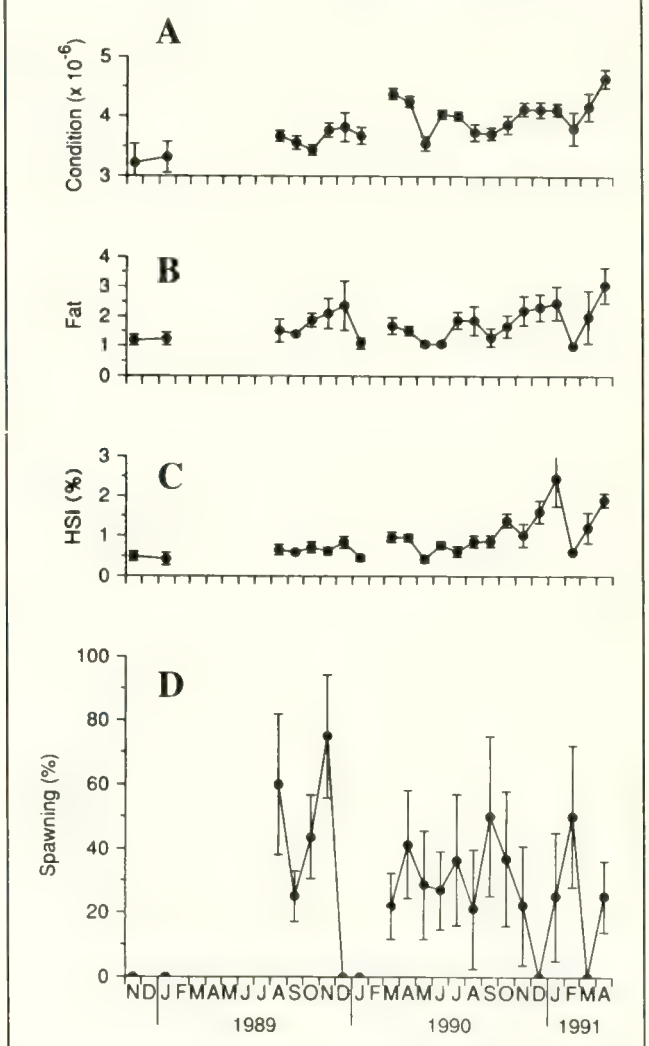

Figure 3

Monthly variation (±95% confidence limits) in (**A**) condition, (**B**) visceral fat index, (**C**) hepatosomatic index and (**D**) proportion spawning of female *Herklotsichthys quadrimaculatus* from Kiribati between November 1988 and April 1991.

higher at Butaritari (1.41 ± 0.06; N=57) than at other sites (Abaiang HSI=1.07 ± 0.11; N=7; Tarawa HSI=0.81 ± 0.09; N=14). The proportion of male *S. delicatulus* that had GSI greater than 5% was also higher at Butaritari (36%) than at other sites (Abaiang 17.5%; Tarawa 20%).

Oocyte weights of *A. sirm* and *S. delicatulus* differed significantly from site to site (Table 7). In *S. delicatulus*, we found the greatest oocyte weight at Abemama and Abaiang — significantly higher than at Butaritari and Tarawa (P<0.01). Oocyte weights in *A. sirm* were also higher at Abaiang (P<0.001; Table 7). We found no significant differences among sites for oocyte weights of *H. quadrimaculatus*.

Sex ratio The sex-ratio of *A. sirm*, *H. quadrimaculatus*, and *S. delicatulus* changed as fish grew but only among the largest length classes of each species were there significant deviations from a ratio of 1:1. In all three species, females dominate the largest length classes (Fig. 6). In our samples, we found significantly more female *A. sirm* and *S. delicatulus* among fish larger than the length at first spawning (180 and 45 mm respectively). With *H.*

Table 4

Mean hepatosomatic index (HSI: %), visceral fat index (Fat) and condition (K: dry weight/length^3) of *Amblygaster sirm*, *Herklotsichthys quadrimaculatus* and *Spratelloides delicatulus* at different stages of gonadal development (SE = standard error ± N = number of females examined).

Species	Stage	HSI ± SE	Fat ± SE	K (× 10–6) ±SE	N
A. sirm	maturing	0.38 ± 0.06	3.4 ± 0.6	4.05 ± 0.25	8
	ripe	0.43 ± 0.04	3.2 ± 0.3	4.14 ± 0.07	30
	spawning	0.39 ± 0.06	2.6 ± 0.4	4.03 ± 0.13	16
	spent	0.42 ± 0.05	1.7 ± 0.2	2.77 ± 0.13	6
H. quadrimaculatus	maturing	0.87 ± 0.08	1.4 ± 0.1	3.89 ± 0.05	45
	ripe	0.96 ± 0.06	1.6 ± 0.1	3.81 ± 0.05	127
	spawning	1.04 ± 0.07	1.8 ± 0.1	3.91 ± 0.05	95
	spent	0.69 ± 0.04	1.7 ± 0.1	3.53 ± 0.06	40
S. delicatulus	maturing	1.41 ± 0.19	1.3 ± 0.2	2.36 ± 0.06	15
	ripe	1.98 ± 0.10	1.6 ± 0.1	2.51 ± 0.04	41
	spawning	1.84 ± 0.15	1.3 ± 0.1	2.46 ± 0.04	35
	spent	1.46 ± 0.10	1.2 ± 0.1	2.28 ± 0.04	55

quadrimaculatus, females dominated among fish over 80 mm (Fig. 6).

Egg production The number of spawnings per month and the daily egg production of all species generally followed the pattern of the proportion spawning (Fig. 7). We found lower daily egg production in *A. sirm* than in the other species. During the period of maximum spawning activity, *A. sirm* and *H. quadrimaculatus* spawned up to 20 times per month (Fig. 7), and *S. delicatulus* spawned daily.

Reproductive life span The reproductive life span of *A. sirm* was significantly longer in Tarawa (60.1 ± 15.4 days) than at the other sites during 1989–90 (P<0.01; Table 8). Similarly, we found *H. quadrimaculatus* had a longer reproductive life span at Abemama (141.8 ± 30.9 days) than at other sites during 1989–91 (P<0.01; Table 8). During the same period, the reproductive life span of *S. delicatulus* was similar at all sites (57.5 ± 4.6 days). However, the reproductive life span of *S. delicatulus* at Tarawa varied significantly between years; fish caught during 1990–91 were not as old as those in previous years (P<0.05; Table 8). No corresponding pattern was observed in *H. quadrimaculatus* from Tarawa. *Herklotsichthys quadrimaculatus* and *S. delicatulus* lived significantly longer after maturity than *A. sirm* (P<0.01).

Our estimates of maximum lifetime egg production of *A. sirm* were similar at the two sites (Abaiang and Tarawa). *Herklotsichthys quadrimaculatus* had higher lifetime egg production at all sites than did co-occurring *S. delicatulus*. The number of days between successive spawnings influenced estimates of lifetime egg production. Although longer in *A. sirm*, the difference was not significant (Table 8).

Recruitment *Amblygaster sirm* recruited from a single protracted period in Kiribati during 1989 (March to October; Fig. 8). We found a greater proportion of survivors had been born between March and July than in all other months except September (P<0.05). There were insufficient data to compare monthly egg production with recruitment, but the period of highest recruitment corresponded with the times of greatest spawning activity. However, this did not appear to be directly related to the absolute number of oocytes produced (Fig. 7).

The proportion of *H. quadrimaculatus* born each month differed over the four years (P<0.05; Fig. 9). In 1976, the greater proportion were born from November to March, while in 1983 over 40% were born during July. Fish caught during 1989–90 showed a different pattern. The highest proportion in 1989 were born in May, whereas in 1990 the highest proportion were born in January. Over all 4 years' data, December (15.4%) and July (13.7%) had the greatest mean proportion of births (P<0.05), but the July value may be biased by the large value in 1983 (Fig. 10). Where data were comparable, we found no relationship between proportion of annual recruitment and monthly egg production (r_s=0.70, P<0.10, N=6 in 1989; r_s=–0.15, P>0.5, N=11 in 1990).

The proportion of *S. delicatulus* born each month varied considerably among the four years examined (Fig. 10). December had the highest proportion of births in 1976. In 1983, most fish were born between May and August, and a similar pattern was found in 1989. By comparison, the distribution of birthdates was more evenly spread in 1990 (Fig. 10). The months with the largest mean proportion across the four years were May (11.2%), June (14.9%), July (15.8%), and December (11.9%). We found a negative relationship between the proportion of births and egg production in 1990 (r_s=–0.58; P<0.05, N=10).

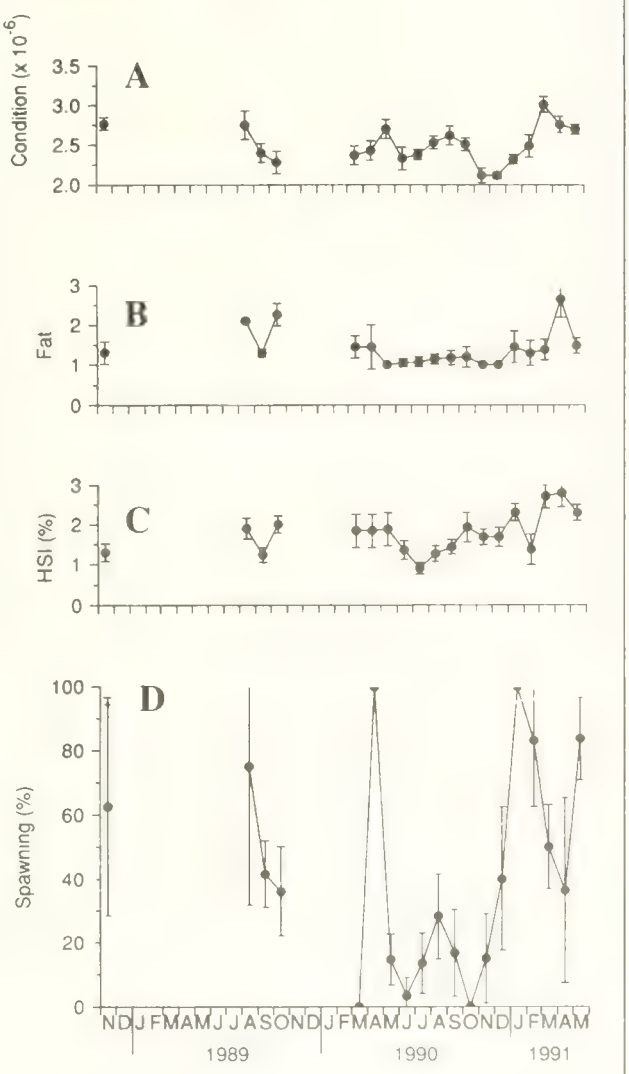

Figure 4

Monthly variation (±95% confidence limits) in (**A**) condition, (**B**) visceral fat index, (**C**) hepatosomatic index and (**D**) proportion spawning of female *Spratelloides delicatulus* from Kiribati between November 1988 and May 1991.

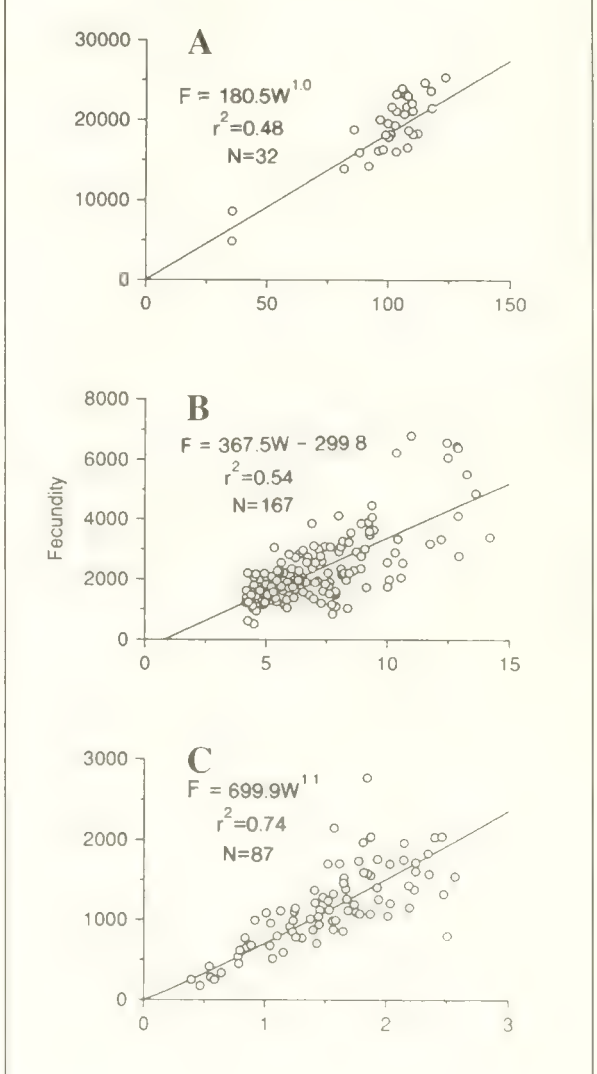

Figure 5

The relationship between batch fecundity and fish weight for (**A**) *Amblygaster sirm*, (**B**) *Herklotsichthys quadrimaculatus* and (**C**) *Spratelloides delicatulus* from Kiribati.

Discussion

The reproductive cycles of *A. sirm*, *H. quadrimaculatus*, and *S. delicatulus* in Kiribati are similar to that reported for temperate multiple-spawning clupeoids (Hunter and Goldberg, 1980; Gil and Lee, 1986; Shelton, 1987; Alheit, 1989). Most studies on multiple spawning clupeoids have been on engraulids; these species spawn many batches of eggs each year and have variable batch fecundity (Alheit, 1989). Our results for *H. quadrimaculatus* and *S. delicatulus* from Kiribati agree with previous reproductive studies of these species in tropical areas (McCarthy, 1985[1]; Moussac and Poupon, 1986; Milton and Blaber, 1991). In the tropics, both species spawn throughout the year, but have periods when spawning activity is greater. In more temperate parts of their range, the reproductive season of both *H. quadrimaculatus* and *S. delicatulus* is shorter and coincides with increases in water temperature in early summer (Williams and Clarke, 1983; Lewis et al., 1983; Conand, 1988).

Table 5

Mean length (mm), age (years), fecundity, relative fecundity (eggs g^{-1}) of *Amblygaster sirm*, *Herklotsichthys quadrimaculatus*, and *Spratelloides delicatulus* and other tropical and subtropical clupeids (sardines, herrings, and sprats) (K = Kiribati, SI = Solomon Islands, I = India, P.N.G. = Papua New Guinea, UK = United Kingdom, SU = Soviet Union, G = Germany).

Species	Site	Length ± SE	Age ± SE	Fecundity ± SE	Rel. fecundity ± SE	*N*	Source
Sardines							
Amblygaster sirm	Abaiang (K)	189 ± 5	0.97 ± 0.03	18789 ± 2757	187.1 ± 25.3	7	(1)
	Tarawa (K)	194 ± 1	1.04 ± 0.03	20327 ± 1391	192.0 ± 12.0	25	(1)
	New Caledonia	139–177	0.90–2.2	8000–27780	300.0 ± 16.9	24	(2), (3)
Sardinella brasiliensis	Brazil	162 ± 2	—	23318 ± 2065	356 ± 37	23	(4)
S. marquesensis	Marquesas Is.	109 ± 6	—	4150 ± 1000	—	6	(5)
S. zunasi	Korea	75–142	1–3	8800–58800	—	31	(6)
Herrings							
Herklotsichthys quadrimaculatus	Hawaii	80–121	—	1155–6296	160–311	46	(7)
	Marshall Is.	100 ± 2	0.59 ± 0.02	4755 ± 380	—	7	(8)
	Butaritari (K)	75 ± 1	0.45 ± 0.01	1844 ± 108	295.5 ± 12.1	44	(1)
	Abaiang (K)	75 ± 1	0.45 ± 0.02	1975 ± 133	317.4 ± 19.3	27	(1)
	Tarawa (K)	76 ± 1	0.44 ± 0.02	2353 ± 110	344.1 ± 10.2	63	(1)
	Abemama (K)	84 ± 2	0.61 ± 0.04	3008 ± 207	319.1 ± 22.7	33	(1)
	Andaman Is. (I)	95–115	—	8353 ± –	—	19	(9)
	Seychelles	88–127	—	4500–8000	—	24	(10)
Opisthonema libertate	Mexico	142 ± 1	—	57125 ± 1850	553 ± 14	115	(11)
Sprats							
Spratelloides delicatulus	Butaritari (K)	52 ± 2	0.27 ± 0.01	1359 ± 143	867 ± 55	19	(1)
	Abaiang (K)	52 ± 1	0.21 ± 0.02	973 ± 43	667 ± 35	7	(1)
	Tarawa (K)	54 ± 1	0.29 ± 0.01	1255 ± 54	735 ± 25	49	(1)
	Abemama (K)	41 ± 1	0.20 ± 0.02	524 ± 95	702 ± 75	12	(1)
	Munda (SI)	48 ± 1	0.26 ± 0.01	799 ± 45	554 ± 25	57	(12)
	Vona Vona (SI)	49 ± 1	0.26 ± 0.01	925 ± 102	717 ± 45	28	(12)
	Tulagi (SI)	46 ± 1	0.21 ± 0.01	926 ± 93	567 ± 49	28	(12)
	New Caledonia	45	—	710	883 ± 14	20	(2)
	India	40 ± 3	—	608 ± 54	—	15	(13)
S. gracilis	Munda (SI)	50	0.19	514	504	1	(14)
	Vona Vona (SI)	37 ± 1	0.15 ± 0.01	505 ± 51	882 ± 68	13	(12)
	P.N.G.	53 ± 2	–	2592 ± 313	1690 ± 96	18	(15)
	Maldives	59 ± 1	0.29 ± 0.02	1998 ± 137	1073 ± 54	33	(12)
	India	40 ± 5	—	790 ± 71	962 ± 53	15	(13)
S. lewisi	Munda (SI)	44 ± 1	0.18 ± 0.01	887 ± 20	925 ± 16	219	(14)
	Vona Vona (SI)	42 ± 1	0.14 ± 0.01	930 ± 51	1032 ± 36	62	(14)
	Tulagi (SI)	49 ± 1	0.28 ± 0.02	1290 ± 84	1230 ± 69	29	(14)
Sprattus sprattus	Scotland (UK)	108	3	2729	187	64	(16)
	Baltic Sea (SU)	121	1.9	2174	232	46	(17)
	North Sea (G)	—	2	—	413	–	(17)

Sources: (1) present study, (2) Conand (1988), (3) Conand (1991), (4) Isaac-Nahum et al. (1988), (5) Nakamura and Wilson (1970), (6) Gil and Lee (1986), (7) Williams and Clarke (1983), (8) Hida and Uchiyama (1977), (9) Marichamy (1971), (10) Moussac and Poupon (1986), (11) Torres-Villegas and Perezgomez (1988), (12) Milton et al. (1990), (13) Mohan and Kunhikoya (1986), (14) Milton unpubl. data, (15) Dalzell (1985), (16) De Silva (1973), (17) Alheit (1988).

Although we found *A. sirm* also had an extended spawning season in Kiribati, the species may not spawn throughout the year. Our result differs from previous studies that found the spawning season lasted two to five months during early summer (Conand, 1991) or the monsoon period (Rosa and Laevastu, 1960; Dayaratne and Gjosaeter, 1986). Neither temperature nor rainfall appear to be the

proximate stimuli for spawning of *A. sirm* in Kiribati. Temperature was constant throughout the year and rainfall was higher at all sites in Kiribati between December and April, when spawning activity was lowest. Most spawning activity in this species occurred during the second half of the year when the prevailing wind direction changed from east to west, associated with the northwest monsoon that starts at this time (Burgess, 1987[5]). Our limited wind and rainfall data did not indicate that increased spawning activity in *A. sirm* was related to the shift in weather pattern.

Gonad maturation and spawning were also linked to changes in fish liver-weight (HSI), visceral fat, and condition of each species. Either HSI or fat index and condition were all significantly reduced in postspawning fish. *Amblygaster sirm* stores energy in the viscera rather than in the liver. Other multiple-spawning clupeoids also transfer energy from stored fat to reproductive tissue (Dahlberg, 1969; Okera, 1974; Hunter and Leong, 1981). In contrast, spent *H. quadrimaculatus* and *S. delicatulus* had reduced HSI, which suggests that the liver is the energy store utilized during reproduction (Diana and MacKay, 1979; Smith et al., 1990). Energy stored in this organ would be readily available for rapid assimilation; hence, fish could spawn multiple batches of eggs rapidly.

Studies of temperate herring, *Clupea harengus*, have shown that gonad maturation is linked to food availability and fat storage (Linko et al., 1985; Henderson and Almatar, 1989; Rajasilta, 1992). Ovaries of all three species in Kiribati and of *S. delicatulus* in the Solomon Islands (Milton and Blaber, 1991) vary in a similar way to herring. Milton and Blaber (1991) did not find a direct relation between spawning and prey availability. This suggests that while gonad maturation in these clu-

[5] Burgess, S. M. 1987. The climate of western Kiribati. New Zealand Meterological Service, Wellington, NZ. Miscellaneous publ. 188, part 7.

Table 6

Stepwise regression of the relationship between various endogenous factors and fish fecundity from sites in Kiribati. (Cr_p^2 = partial correlation coefficient; r^2 = overall correlation coefficeint; P = significance level; N = sample size; HSI = hepatosomatic index; All = data from each site combined).

Species	Site	Factor	r_p^2	r^2	P	N
Amblygaster sirm	Tarawa	Weight	0.24	0.44	<0.05	25
		HSI	0.20			
	All	Weight	0.38	0.64	<0.001	32
		Condition	0.28			
Herklotsichthys quadrimaculatus	Butaritari	Weight	0.36	0.43	<0.001	44
		Condition	0.07			
	Abaiang	Weight	0.28	0.39	<0.01	27
		HSI	0.11			
	Tarawa	Length	0.58	0.63	<0.001	63
		Condition	0.03			
		Age	0.02			
	Abemama	Weight	0.62	0.72	<0.001	33
		Fat	0.10			
	All	Weight	0.54	0.57	<0.001	167
		Fat	0.03			
Spratelloides delicatulus	Butaritari	Weight	0.70	0.76	<0.001	19
		HSI	0.06			
	Abaiang	no factor				7
	Tarawa	Weight	0.37	0.52	<0.001	49
		HSI	0.15			
	Abemama	Weight	0.87	0.87	<0.001	12
	All	Weight	0.59	0.66	<0.001	87
		HSI	0.07			

Table 7

Mean hydrated oocyte dry weight of *Amblygaster sirm*, *Herklotsichthys quadrimaculatus*, and *Spratelloides delicatulus* from four sites in Kiribati (N = number of females examined).

Species	Site	Hydrated oocyte weight ± SE (× 10^{-4} g)	N
A. sirm	Abaiang	4.4 ± 0.5	7
	Tarawa	1.5 ± 0.1	16
H. quadrimaculatus	Butaritari	2.0 ± 0.2	36
	Abaiang	1.8 ± 0.1	12
	Tarawa	1.6 ± 0.2	19
	Abemama	1.9 ± 0.2	26
S. delicatulus	Butaritari	0.7 ± 0.1	11
	Abaiang	1.4 ± 0.2	12
	Tarawa	0.8 ± 0.04	27
	Abemama	2.2 ± 0.2	10

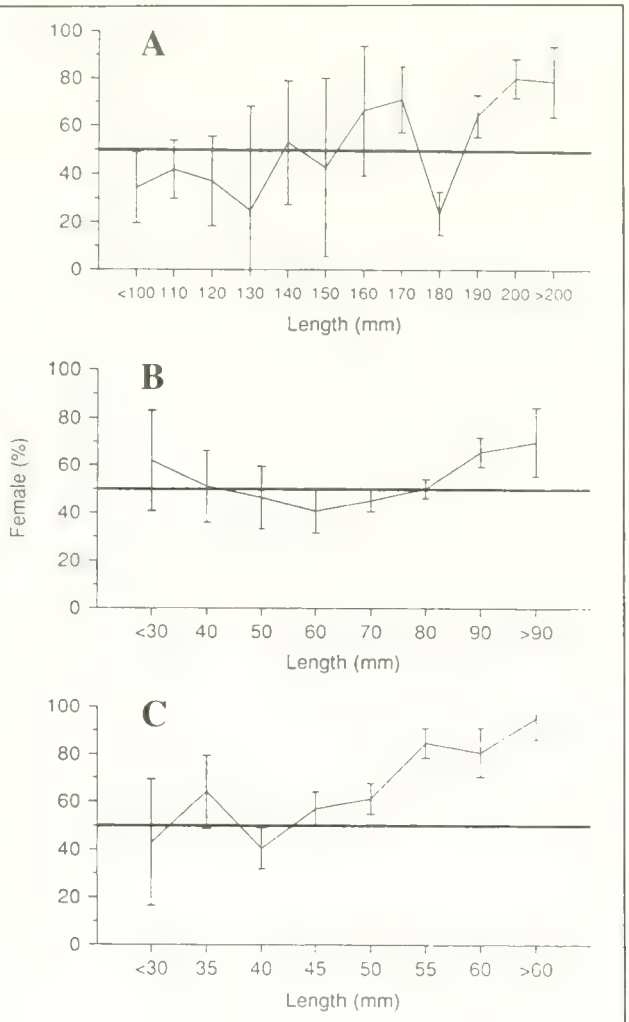

Figure 6

Ontogenetic change in the proportion female of (**A**) *Amblygaster sirm*, (**B**) *Herklotsichthys quadrimaculatus* and (**C**) *Spratelloides delicatulus* (±95% confidence limits) from Kiribati.

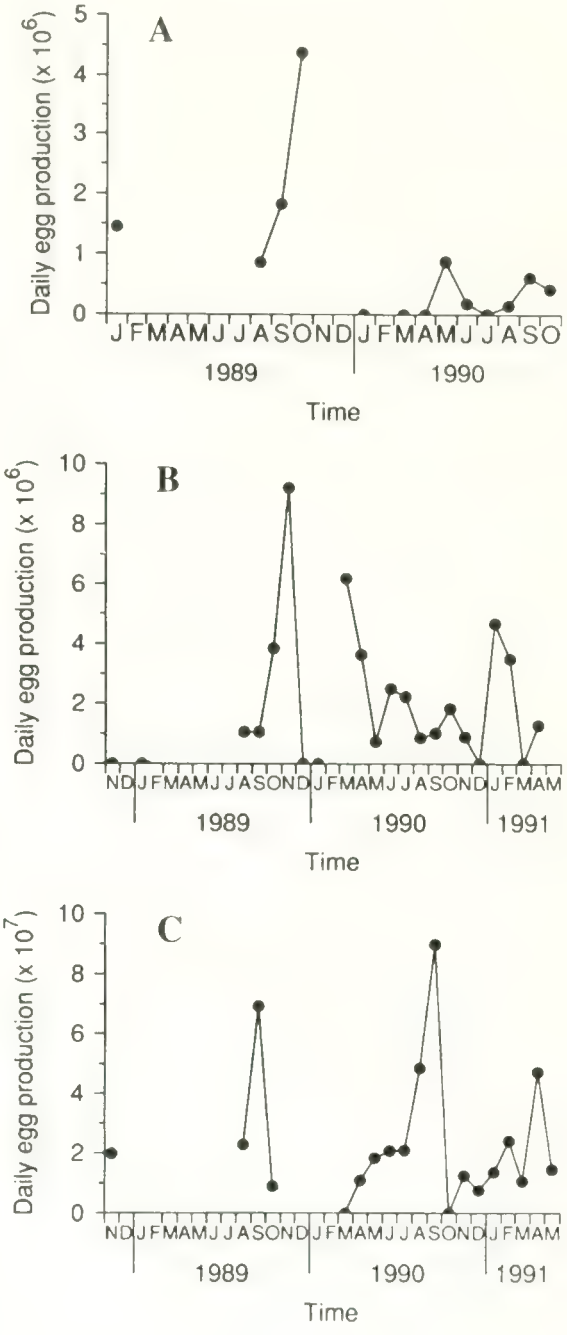

Figure 7

Monthly estimates of daily egg production of (**A**) *Amblygaster sirm*, (**B**) *Herklotsichthys quadrimaculatus* and (**C**) *Spratelloides delicatulus* from Kiribati during the study period.

peids is probably linked to cycles in prey abundance, fat storage may reduce the effects of short-term fluctuations in prey abundance on reproduction.

Diel timing of spawning events was similar for all species. We found new post-ovulatory follicles (day-0) in females collected from 2130 hours onwards with the greatest proportion detected after 0100. This indicates that these species spawn during the early part of the night, probably prior to midnight. Our results are consistent with previous studies that found high densities of *A. sirm* eggs in the plankton after midnight (Delsman, 1926; Lazarus, 1987). Studies of other sardines (Goldberg et al., 1984; Isaac-Nahum et al., 1988; Re et al., 1988) and tropical clupeoids (Clarke, 1987) also showed that spawning peaked before midnight.

Length and age at sexual maturity of *A. sirm* and *H. quadrimaculatus* in Kiribati differed from those

Table 8

Mean reproductive life span (in days) and days between spawning of *Amblygaster sirm*, *Herklotsichthys quadrimaculatus*, and *Spratelloides delicatulus* from four sites in Kiribati (N = number of length-frequency samples; No. = number of months examined).

Species	Site	Year	Reproductive life span ± SE	Range	N	Days between spawning	Range	No	Max. lifetime egg production ($\times 10^4$)
A. sirm	Abaiang	1989–1990	19.0 ± 6.4	0–66	12				20.0
	Tarawa	1989–1990	60.1 ± 15.4	0–127	7				41.6
	Abemama	1989–1990	3.2 ± 3.1	0–19	6				
Overall	1989–1990	26.7 ± 6.8	0–127	25	6.2 ± 2.3	1.5–25.9	10	38.7	
H. quadrimaculatus	Butaritari	1989–1991	47.3 ± 15.0	0–201	14				11.9
	Abaiang	1989–1991	73.9 ± 15.6	0–201	17				12.8
	Tarawa	1976/83/89–91	84.1 ± 7.8	0–254	64				19.3
	Abemama	1989–1991	141.8 ± 30.9	0–286	12				27.7
	Overall	1989–1991	80.6 ± 8.6	0–286	74	3.1 ± 0.3	1.3–4.7	15	21.1
S. delicatulus	Butaritari	1989–1991	53.6 ± 4.6	24–74	15				1.9
	Abaiang	1989–1991	49.2 ± 5.1	21–80	11				1.5
	Tarawa	1989–1991	66.9 ± 10.6	0–144	16				3.5
	Tarawa	1976	76.6 ± 10.5	45–129	7				3.1
	Tarawa	1983/84	84.3 ± 9.5	34–152	16				3.7
	all	1989	90.0 ± 13.4	53–144	7				3.2
	all	1990/91	51.0 ± 4.1	0–109	35				2.5
	Overall	1989–1991	57.5 ± 4.6	0–144	42	5.2 ± 1.8	1–30	16	3.2

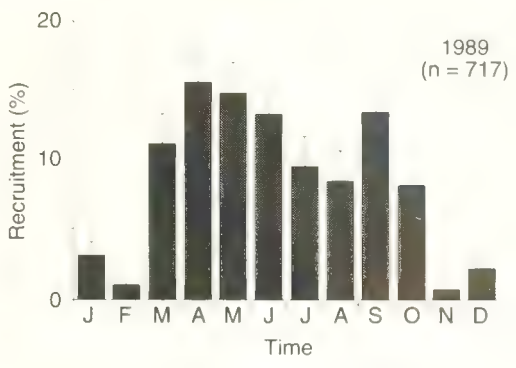

Figure 8

The proportion of *Amblygaster sirm* (±95% confidence limits) sampled between August 1989 and July 1990 born each month in 1989, backcalculated from length-frequency samples.

in other parts of their range (Table 3). We found few differences within Kiribati, but both species became sexually mature and spawned at much shorter body lengths than at other locations. *Herklotsichthys quadrimaculatus* did not grow as large in Kiribati as elsewhere (Milton et al., 1993), but the proportion of maximum size at which this species matured was similar throughout its range. Milton and Blaber (1991) found regional differences in length at sexual maturity in other small tropical clupeoids; they suggested these differences were consistent with the hypothesis of Longhurst and Pauly (1987) that fish of any species living in cooler water will grow to and mature at a larger size through the interaction of oxygen supply and demand. Our data on *H. quadrimaculatus* is consistent with this hypothesis — the other studies were all at sites at higher latitudes than Kiribati, where the water temperature is lower. Also, the proportion of maximum size at which fish matured was similar at all locations, despite the absolute differences in size at maturity in Kiribati.

By comparison, *A. sirm* matured at a smaller size and grew to a larger size in Kiribati than at other locations (Milton et al., 1993). The proportion of maximum size at which fish matured was also lower than found in previous studies and was less than the proportion common to a wide range of clupeoids (70%; Beverton, 1963). In response to severe fishing pressure, the size and age at sexual maturity of several sardine species have been found to decline (Murphy, 1977). Presumably, this is because any density-dependent effects are reduced during early growth (Beverton and Holt, 1957; Ware, 1980). *Amblygaster sirm* can have high or variable adult mortality in Kiribati (Rawlinson et al., 1992), favouring early maturation (Stearns and Crandall, 1984).

Length at first spawning was a similar proportion of maximum size for the three species and was con-

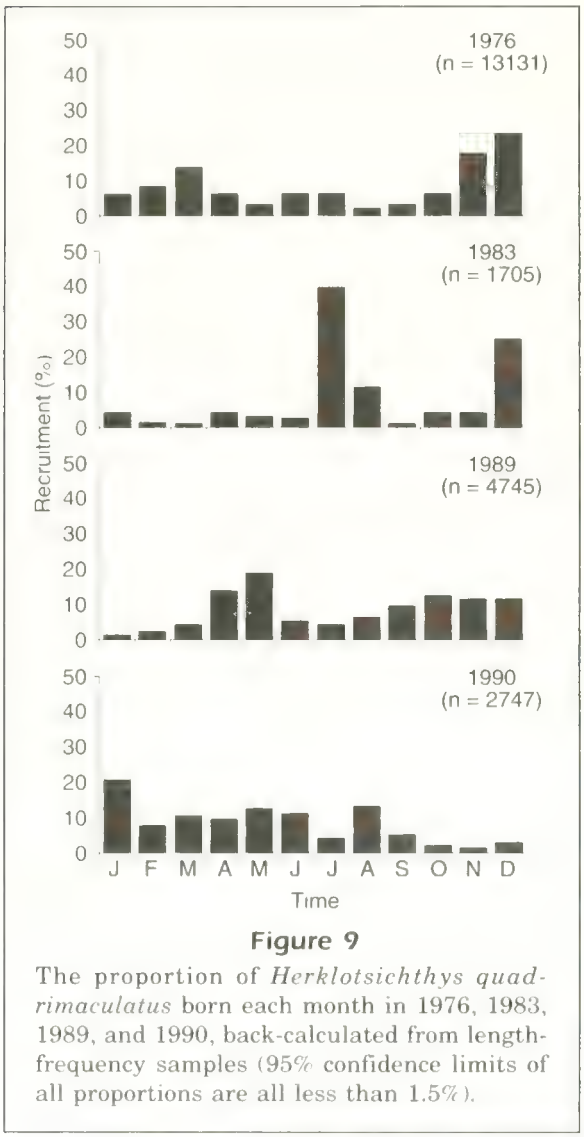

Figure 9

The proportion of *Herklotsichthys quadrimaculatus* born each month in 1976, 1983, 1989, and 1990, back-calculated from length-frequency samples (95% confidence limits of all proportions are all less than 1.5%).

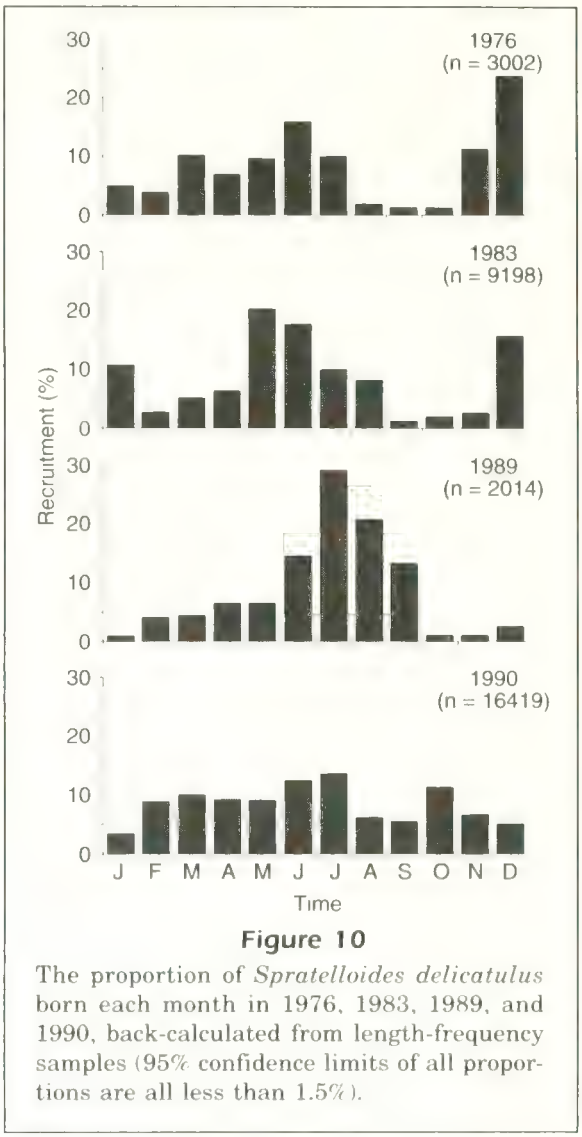

Figure 10

The proportion of *Spratelloides delicatulus* born each month in 1976, 1983, 1989, and 1990, back-calculated from length-frequency samples (95% confidence limits of all proportions are all less than 1.5%).

sistent with the close relation with maximum size found by Blaxter and Hunter (1982) for other clupeoids. These authors also noted a latitudinal effect; fish from lower latitudes spawned at a smaller proportion of maximum size.

Temperate clupeids (especially herrings, *Clupea* spp.) show a great plasticity in the number and size of eggs produced; many species show seasonal, and inter-annual, as well as geographic, variation in their reproductive outputs (Alheit, 1989; Jennings and Beverton, 1991) reflecting energetic resources and environmental conditions (Hay and Brett, 1988; Henderson and Almatar, 1989). By comparison, the tropical herring, *H. quadrimaculatus*, spawned throughout the year and showed negligible temporal or spatial variation in fecundity, egg weight, or inter-spawning interval. This indicates that egg production was almost constant throughout the study period and suggests that adult food resources and larval survival are predictable or relatively constant (Sibly and Calow, 1983).

In comparison to other species, *S. delicatulus* had a higher relative fecundity that was also correlated with HSI. Females in spawning condition also had a higher HSI at Butaritari. Commercial CPUE was highest at this site (Rawlinson et al., 1992) and *S. delicatulus* spawned more, smaller eggs than at other sites where relative fecundity was lower. These data suggest that the fecundity of *S. delicatulus* may be influenced by the amount of energy stored in the liver. This energy store would be important in a small multiple-spawning species; it would enable the fish to continue spawning during short periods of reduced food supply (Hay and Brett, 1988). The length of the inter-spawning interval has been shown experimentally to be related

to food supply in other fish species (Townshend and Wootton, 1984). Fish at Butaritari may experience a more predictable environment that enables them to produce more eggs of smaller size than fish in more variable environments.

In contrast, *A. sirm* delayed spawning beyond the size and age at sexual maturity and did not spawn until one year old. As fecundity was related to weight, delayed spawning enabled *A. sirm* to grow faster than the other species (Milton et al., 1993) and have a higher batch fecundity when spawning started. Murphy (1968) hypothesized that delayed spawning and longer reproductive life span would evolve in response to variable reproductive success. However, Armstrong and Shelton (1990) demonstrated that, even with a short reproductive life span, multiple spawners had a high probability of successful reproduction when subject to random environmental fluctuations over time. Thus, delaying spawning would be of adaptive advantage if mortality was low (Roff, 1984) because batch fecundity and lifetime egg production would be increased.

Our estimates of the reproductive lifespan of *A. sirm* indicate that this species spawns fewer times in their lifetime than other species and thus would also have less chance of successful spawning than other species. Given that this is the longest-lived of the species examined, our estimate of overall mean lifespan may be biased by the small number of months sampled. Large fish may be under-represented in small catches and may contribute to underestimating the reproductive potential of *A. sirm*.

Herklotsichthys quadrimaculatus had a longer reproductive life span and spawned more frequently than did the other species. Reproductive life span varied little among sites (except Abemama) and there was no significant temporal variation, which suggests that survival rates of large adult *H. quadrimaculatus* are fairly constant in Kiribati. This is reflected in their life-history parameters, which varied little among sites or over time. In contrast, the frequency distribution of back-calculated birthdates indicated that overall survival was variable both between and within years, and was not related to monthly egg production. We have no estimates of adult abundance during the study period, and so population egg production could not be assessed. However, the annual CPUE and abundance of *H. quadrimaculatus* in the baitfishery were similar in the three years for which both data sets were available (Rawlinson et al., 1992). This suggests that population size was relatively constant during this period. If so, then variation in post-hatching survival probably has an important influence on recruitment in this species (Smith, 1985).

The reproductive life span of the smallest species, *S. delicatulus*, was intermediate between the other species and varied little among sites during 1989 and 1990. Unlike *H. quadrimaculatus*, the reproductive life span of *S. delicatulus* varied between years, which suggests that survival rates are not as constant or as predictable as those of *H. quadrimaculatus*. Potential lifetime egg production of each female was only one tenth that of other species, but, because of the larger number of females, monthly estimates of daily egg production were higher. The distribution of back-calculated birthdates varied between years, but a greater proportion of births fell in May-August, irrespective of the pattern of egg production. Annual CPUE of *S. delicatulus* (Rawlinson et al., 1992) was similar in 1989 and 1990, which suggests that fishing mortality had not contributed to the increased mortality that reduced the reproductive life span in 1990.

The reproduction and abundance of *S. delicatulus* may be more directly influenced by its environment than are the other species. Adult survival is variable and low (Tiroba et al., 1990); egg production varies, probably in response to food supply, and survival to recruitment is unpredictable. Yet the potential for successful reproduction with this strategy may still be relatively high (Armstrong and Shelton, 1990). In contrast, *H. quadrimaculatus* appears to be able to offset environmental variability to produce a relatively constant supply of eggs.

The distribution pattern of back-calculated birthdates of each species was not consistent among species. Months when a higher proportion survived differed for each species during all years; months with highest mean survival were not the same for any species. This suggests that the effects of environmental conditions such as seasonal food availability or favorable physical conditions are not the same for each species. Alternatively, other factors such as predation (Rawlinson et al., 1992) may have greater influence on survival to recruitment. Egg production by *S. delicatulus* was positively correlated to survival rates in 1989 and negatively correlated in 1990. This seems unrelated to fish abundance as catch rates were higher in 1989 than in 1990 (Rawlinson et al., 1992).

Large variations in recruitment, reflected in catch rates of the main baitfishes do not appear to be directly linked with variations in egg production. All spawn in the lagoon for most of the year, and distribution of birthdates indicated recruitment in most months. Although the absolute level of recruitment varied throughout the year, multiple spawning reduces fluctuations in population size due to environmental variability and should ensure that relatively

stable population sizes are maintained. Earlier studies of *A. sirm* and *H. quadrimaculatus* in Tarawa lagoon suggested that these species spend at least part of their life outside the lagoon (R. Cross, 1978[4]; McCarthy, 1985[1]). If this is the case, fluctuations in the relative abundances of these species may be related to migrations; a better understanding of the factors causing large-scale movements is necessary before predicting the potential yield of this fishery.

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Literature cited

Alheit, J.
1988. Reproductive biology of sprat (*Sprattus sprattus*): factors determining annual egg production. J. Cons. int. Explor. Mer 44:162–168.
1989. Comparative spawning biology of anchovies, sardines, and sprats. Rapp. P.-v. Reun. Cons. int. Explor. Mer 191:7–14.

Armstrong, M. J., and P. A. Shelton.
1990. Clupeoid life-history styles in variable environments. Envir. Biol. Fish 28:77–85.

Armstrong, M. J., P. A. Shelton, I. Hampton, G. Jolly, and Y. Melo.
1988. Egg production estimates of anchovy biomass in the southern Benguela system. Calif. Coop. Oceanic Fish. Invest. Rep. 26:3040.

Beverton, R. J. H.
1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. Rapp. P-V. Reun. Cons. int. Explor. Mer 154:44–67.

Beverton, R. J. H., and S. J. Holt.
1957. On the dynamics of exploited fish populations. Fish Invest., Ser. 2, Mar. Fish. GB Minist. Agric. Fish. Food 19:1–533.

Blaxter, J. S. H., and J. R. Hunter.
1982. The biology of the clupeoid fishes. Adv. in Mar. Biol. 20:1224.

Clarke, T. A.
1987. Fecundity and spawning frequency of the Hawaiian anchovy or Nehu, *Encrasicholina purpurea*. Fish. Bull. 85:127–138.
1989. Seasonal differences in spawning, egg size, and early development time of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. Fish Bull. 87:593–600.

Conand, F.
1988. Biology and ecology of small pelagic fish from the lagoon of New Caledonia usable as bait for tuna fishing. Thesis Studies, ORSTOM, Paris, 239 p.
1991. Biology and phenology of *Amblygaster sirm* (Clupeidae) in New Caledonia, a sardine of the coral environment. Bull. Mar. Sci. 48:137–149.

Conover, W. J.
1980. Practical nonparametric statistics, 2nd ed. J. Wiley & Sons, NY, 493 p.

Cushing, D. H.
1967. The grouping of herring populations. J. Mar. Biol. Assoc. U.K. 47:193–208.
1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. int. Explor. Mer 33:340–362.

Cyrus, D. P., and S. J. M. Blaber.
1984. The reproductive biology of *Gerres* in Natal estuaries. J. Fish. Biol 24:491–504.

Dahlberg, M. D.
1969. Fat cycles and condition factors of two species of menhaden, *Brevoortia* (Clupeidae), and natural hybrids from the Indian river of Florida. Am. Midl. Nat. 82:117–126.

Dalzell, P.
1985. Some aspects of the reproductive biology of *Spratelloides gracilis* (Schlegel) in the Ysabel Passage, Papua New Guinea. J. Fish. Biol. 27:229–237.

Dalzell, P., S. Sharma, and J. Prakash.
1987. Preliminary estimates of the growth and mortality fo three tuna baitfish species, *Herklotsichthys quadrimaculatus, Spratelloides delicatulus* and *Rhabdamia gracilis* from Fijian waters. Tuna Billfish Assessment Programme Tech. Rep. 20:1–15.

Dayaratne, P., and J. Gjosaeter.
1986. Age and growth of four *Sardinella* species from Sri Lanka. Fish. Res. 4:1–33.

Delsman, H. C.
1926. Eggs and larvae from the Java Sea: 7, The genus *Clupea*. Treubia 8:218–239.

De Silva, S. S.
1973. Aspects of the reproductive biology of the sprat, *Sprattus sprattus* in inshore waters of the west coast of Scotland. J. Fish Biol. 5:689–705.

Diana, J. S., and W. C. MacKay.
1979. Timing and magnitude of energy deposition and loss in the body, liver and gonads of northern pike (*Esox lucius*). J. Fish. Res. Board. Can. 36:481–487.

Gil, J. W., and T. W. Lee.
1986. Reproductive ecology of the scaled sardine, *Sardinella zunasi* (Family Clupeidae), in Cheonsu Bay of the Yellow sea, Korea. *In* T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura (eds.), Indo-Pacific fish biology: proceedings of the second international conference on Indo-Pacific fishes, p. 818–829. Ichthyological Society of Japan, Tokyo.

Goldberg, S. R., V. H. Alarcon, and J. Alheit.
1984. Postovulatory follicle histology of the Pacific sardine, *Sardinops sagax*, from Peru. Fish. Bull. 82:443–445.

Hay, D. E., and J. R. Brett.
1988. Maturation and fecundity of Pacific herring (*Clupea harengus pallasi*): an experimental study with comparisons to natural populations. Can. J. Fish. Aquat. Sci. 45:399–406.

Henderson, R. J., and S. M. Almatar.
1989. Seasonal changes in the lipid composition of herring (*Clupea harengus*) in relation to gonad maturation. J. Mar. Biol. Assoc. U.K. 69:323–334.

Hida, T. S., and J. H. Uchiyama.
1977. Biology of the baitfishes *Herklotsichthys punctatus* and *Pranesus pinguis* in Majuro, Marshall Islands. *In* R. S. Shomura, (ed.), Collection of tuna baitfish papers. NOAA Technical Report NMFS Circular 408:63–68.

Hobson, E. S., and J. R. Chess.
1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. Fish. Bull. 76:133–153.

Hunter, J. R., and S. R. Goldberg.
1980. Spawning incidence and batch fecundity in northern anchovy *Engraulis mordax*. Fish. Bull. 77:641–652.

Hunter, J. R., and R. Leong.
1981. The spawning energetics of female northern anchovy *Engraulis mordax*. Fish. Bull. 79: 215–230.

Iles, T. D.
1984. Allocation of resources to gonad and soma in Atlantic herring *Clupea harengus*. *In* G. W. Potts and R. J. Wootton (eds.), Fish reproduction: strategies and tactics, p. 331–347. Academic Press, London.

Isaac-Nahum, V. J., R. de D. Cardoso, G. Servo, and C. L. del B. Rossi-Wongtschowski.
1988. Aspects of the spawning biology of the Brazilian sardine, *Sardinella brasiliensis*, (Clupeidae). J. Fish Biol. 32:383–396.

Jennings, S., and R. J. H. Beverton.
1991. Intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus*) stocks. ICES J. Mar. Sci. 48:117–125.

Lazarus, S.
1987. Studies on the early life history of *Sardinella sirm* from Vizhinjam, southwest coast of India. Indian J. Fish. 34:28–40.

Leis, J. M., and T. Trnski.
1989. The larvae of Indo-Pacific shorefishes. N.S.W. Univ. Press, Kensington, NSW, Australia, 371 p.

Lewis, A. D., S. Sharma, J. Prakash, and B. Tikomainiusiladi.
1983. The Fiji baitfishery 1981–82, with notes on the biology of the gold spot herring *Herklotsichthys quadrimaculatus* (Clupeidae), and the blue sprat *Spratelloides delicatulus* (Dussumieriidae). Fish. Div. Min. Agr. Fish. Tech. Rep. Fiji No. 6, 35 p.

Linko, R. R., J. K. Kaitaranta, and R. Vuorela.
1985. Comparison of the fatty acids in Baltic herring and available plankton feed. Comp. Biochem. Physiol. 82B:699–705.

Longhurst, A. R., and D. Pauly.
1987. Ecology of tropical oceans. Academic Press, San Diego, CA, 407 p.

MacInnes, M.
1990. The status of the tuna baitfishery in Kiribati and its impact on the tuna industry. *In* S. J. M. Blaber and J. W. Copland (eds.), Tuna baitfish in the Indo-Pacific region, p. 55–59. ACIAR Proc. 30.

McManus, J. F. A., and R. W. Mowry.
1964. Staining methods: histological and histochemical. Harper Row, New York, NY, 423 p.

Marichamy, R.
1971. Maturity and spawning of the spotted herring, *Herklotsichthys punctatus* from the Andaman sea. Ind. J. Fish. 18:148–155.

Milton, D. A., and S. J. M. Blaber.
1991. Maturation, spawning seasonality, and proximate spawning stimuli of six species of tuna baitfish in the Solomon Islands. Fish. Bull. 89:221–237.

Milton, D. A., S. J. M. Blaber, G. Tiroba, J. L. Leqata, N. J. F. Rawlinson, and A. Hafiz.
1990. Reproductive biology of *Spratelloides delicatulus*, *S. gracilis* and *Stolephorus heterolobus* from Solomon Islands and Maldives. In S. J. M. Blaber and J. W. Copland (eds.), Tuna baitfish in the Indo-Pacific region, p. 89–99. ACIAR Proc. 30.

Milton, D. A., S. J. M. Blaber, and N. J. F. Rawlinson.
1991. Age and growth of three species of tuna baitfish (genus: *Spratelloides*) in the tropical Indo-Pacific. J. Fish Biol. 39:849–866.
1993. Age and growth of three tropical clupeids from Kiribati, central south Pacific. J. Fish Biol. 43:89–108.

Mohan, M., and K. K. Kunhikoya.
1986. Biology of the bait fishes *Spratelloides delicatulus* and *S. japonicus* from Minicoy waters. Cent. Mar. Fish. Res. Inst. Bull. 36: 155–164.

Moussac, G., and J. C. Poupon.
1986. Growth and reproduction of *Herklotsichthys punctatus* (Pisces: Clupeidae) from Seychelles. Cybium 10:31–45.

Murphy, G. I.
1968. Pattern in life history and the environment. Am. Nat. 102:391–403.
1977. Clupeoids. *In* J. A. Gulland (ed.), Fish population dynamics, p. 283–308. J. Wiley & Sons, New York.

Nakamura, E. L., and R. C. Wilson.
1970. The biology of the Marquesan sardine, *Sardinella marquesensis*. Pac. Sci. 24:359–376.

Nikolsky, G. V.
1963. The ecology of fishes. Academic Press, London, 352 p.

Okera, W.
1974. Morphometrics, 'condition' and gonad development of the east African *Sardinella gibbosa* and *Sardinella albella*. J. Fish Biol. 6:801–812.
1982. Observations on the maturation condition of some pelagic fishes from northern Australian waters. CSIRO Marine Lab. Rep. 144:1–15.

Parker, K.
1980. A direct method for estimating northern anchovy, *Engraulis mordax* biomass. Fish. Bull. 78:541–544.
1985. Biomass model for the egg production method. *In* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, p. 5–6. NOAA Technical Report NMFS 36.

Parrish, R. H., D. L. Mallicoate, and R. A. Klingbeil.
1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. Fish. Bull. 84:503–517.

Pauly, D., and M. L. Palomares.
1989. New estimates of monthly biomass, recruitment and related statistics of anchoveta (*Engraulis ringens*) of Peru (4–14RS), 1953–1985. *In* D. Pauly, P. Muck, J. Mendo, and I. Tsukayama (eds.), The Peruvian upwelling ecosystem: dynamics and interactions, p. 189–206. IMARPE and GTZ and ICLARM, Peru.

Peterman, R. M., and M. J. Bradford.
1987. Wind speed and mortality rate of a marine fish, the northern anchovy, *Engraulis mordax*. Science 235:354–356.

Rajasilta, M.
1992. Relationship between food, fat, sexual maturation, and spawning time of Baltic herring (*Clupea harengus membras*) in the Archipelago Sea. Can. J. Fish. Aquat. Sci. 49:644–654.

Rawlinson, N. J. F., D. A. Milton, and S. J. M. Blaber.
1992. Tuna baitfish and the pole-and-line industry in Kiribati. ACIAR Technical Report No. 24, 90 p.

Re, P., A. Farinha, and I. Meneses.
1988. Diel spawning time of sardine, *Sardina pilchardus* (Teleostei, Clupeidae), off Portugal. Inv. Pesq. 52:207–213.

Ricker, W. E.
1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559–623.

Roff, D. A.
1984. The evolution of life history parameters in teleosts. Can. J. Fish. Aquat. Sci. 41:989–1000.

Rosa, H., and T. Laevastu.
1960. Comparison of biological and ecological characteristics of sardines and related species—a preliminary study. *In* H. Rosa and G. Murphy (eds.), Proceedings of the world scientific meeting on the biology of sardines and related species, Vol. 2, p. 521–552. FAO, Rome.

Shelton, P. A.
1987. Life-history traits displayed by neritic fish in the Benguela current ecosystem. *In* A. I. L. Payne, J. A. Gulland, and K. H. Brinks (eds.), The Benguela and comparable ecosystems. S. Afr. J. Mar. Sci. 5:235–242.

Sibly, R., and P. Calow.
1983. An integrated approach to life-cycle evolution using selective landscapes. J. Theor. Biol. 102:527–536.

Smith, P. E.
1985. Year-class strength and survival of 0–group clupeoids. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1):69–82.

Smith, R. L., A. J. Paul, and J. M. Paul.
1990. Seasonal changes in energy and the energy cost of spawning in Gulf of Alaska Pacific cod. J. Fish Biol. 36:307–316.

Sokal, R. R., and F. J. Rohlf.
1981. Biometry, 2nd ed. Freeman and Co., New York, NY, 859 p.

Somerton, D. A.
1990. Baitfish stock assessment using the egg production method: an application on the Hawaiian anchovy or nehu (*Encrasicholina purpurea*). *In* S. J. M. Blaber and J. W. Copland (eds.), Tuna baitfish in the Indo-Pacific region, p. 152–158. ACIAR Proc. 30.

Stearns, S. C., and R. E. Crandall.
1984. Plasticity for age and size at sexual maturity: a lifehistory response to unavoidable stress. *In* G. W. Potts and R. J. Wootton (eds.), Fish reproduction: strategies and tactics, p. 13–33. Academic Press, London.

Tiroba, G., N. J. F. Rawlinson, P. V. Nichols, and J. L. Leqata.
1990. Length-frequency analysis of the major baitfish species in Solomon Islands. *In* S. J. M. Blaber and J. W. Copland (eds.), Tuna baitfish in the Indo-Pacific region, p. 114–134. ACIAR Proc. 30.

Torres-Villegas, J. R., and L. Perezgomez.
1988. Fecundity variation of *Opisthonema libertate* (Pisces: Clupeidae) from 1983 to 1985 in Bahia Magdalena, Baja California, sur Mexico. Inv. Pesq. 52:193–206.

Townshend, T. J., and R. J. Wootton.
1984. Effects of food supply on the reproduction of the convict cichlid, *Cichlasoma nigrofasciatum*. J. Fish Biol. 24:91–104.

Walpole, R. E.
1974. Introduction to statistics, 2nd ed. MacMillan Publ., New York, NY, 340 p.

Ware, D. M.
1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37:1012–1024.

Williams, V. R., and T. A. Clarke.
1983. Reproduction, growth, and other aspects of the biology of the gold spot herring, *Herklotsichthys*

quadrimaculatus (Clupeidae), a recent introduction to Hawaii. Fish. Bull. 81:587–597.

Wright, P. J.

1990. The reproductive strategy of *Stolephorus heterolobus* in the south Java Sea. *In* S. J. M. Blaber and J. W. Copland (eds.), Tuna baitfish in the Indo-Pacific region, p. 83–88. ACIAR Proc. 30.

Young, J. W., S. J. M. Blaber, and R. Rose.

1987. Reproductive biology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. Mar. Biol. 95:323–332.

Examination of stock and school structure of striped dolphin (*Stenella coeruleoalba*) in the eastern Pacific from aerial photogrammetry

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Abstract.—Determination of stock structure for striped dolphins (*Stenella coeruleoalba*) in the eastern Pacific has been problematic, because very few specimens have been available for study. We compared length data obtained from vertical aerial photographs of 28 schools of striped dolphins from the northern and southern regions of the eastern tropical Pacific and found no significant differences in average length for adult animals (≥180cm) or for adult females, defined here as dolphins closely accompanied by a calf. Analyses of back-projected birth dates for dolphins ≥155cm revealed a broad pulse in reproduction extending from the fall through the spring; however, sample size was inadequate to compare timing of reproduction between the two areas. Striped dolphins measured from aerial photographs were longer on average than those killed incidentally in fishing operations. We found a pattern of segregation by size between schools that is analogous to the separate schools of juveniles and adults that are found in the western Pacific. We hypothesized that the specimen data base may be biased because tuna purse-seine fishermen in the eastern tropical Pacific may selectively set on schools composed of younger, smaller dolphins.

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Because striped dolphins, *Stenella coeruleoalba*, are killed incidentally in purse-seine fishing for yellowfin tuna in the eastern tropical Pacific (ETP), the National Marine Fisheries Service (NMFS) is required by the Marine Mammal Protection Act (as amended in 1988) to monitor trends in their abundance (Holt and Sexton, 1989; Wade and Gerrodette, in press). To satisfy this congressional mandate, information on stock structure is required. The determination of stock structure for striped dolphins in the ETP has been particularly difficult because of the small number of animals killed in the tuna fishery and, therefore, small number of specimens available for study (DeMaster et al., 1992). In the absence of morphological, life history, or genetic data to provide evidence of reproductive isolation, stocks of striped dolphins have been identified provisionally based on discontinuities in distribution. With more sighting data from observers aboard fishing vessels and research cruises, the number of proposed stocks has decreased from five or six (Smith, 1979[1]; Holt and Powers, 1982) to one (Dizon et al., in press) pending availability of additional data.

For this report, we examined length data to help clarify the issue of stock structure. These data were extracted from vertical aerial photographs collected during line transect surveys and are thus presumably free of any "sampling" biases associated with the fishery. Here, we compare length samples from aerial photographs of animals from the northern and southern stock regions proposed by Perrin et al. (1985) for evidence of differences in average length or timing of reproduction. Data were then compared with measurements available from specimens killed incidentally in purse-seine fishing. We also examined the frequency distribution of lengths within individual schools. These data were used to test for size-age segregation, as reported for dolphins taken in the drive fishery on the Pacific coast of Japan (Miyazaki, 1977; Miyazaki and Nishiwaki, 1978).

Methods

Length measurements were made on vertical aerial photographs of 28 schools of striped dolphins (Fig. 1). We photographed the schools with a KA-45A military reconnaissance

[1] Smith, T. D. (ed). 1979. Report of the status of porpoise stocks workshop; 27–31 August, La Jolla, California. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep., LJ-79-41, 120 p.

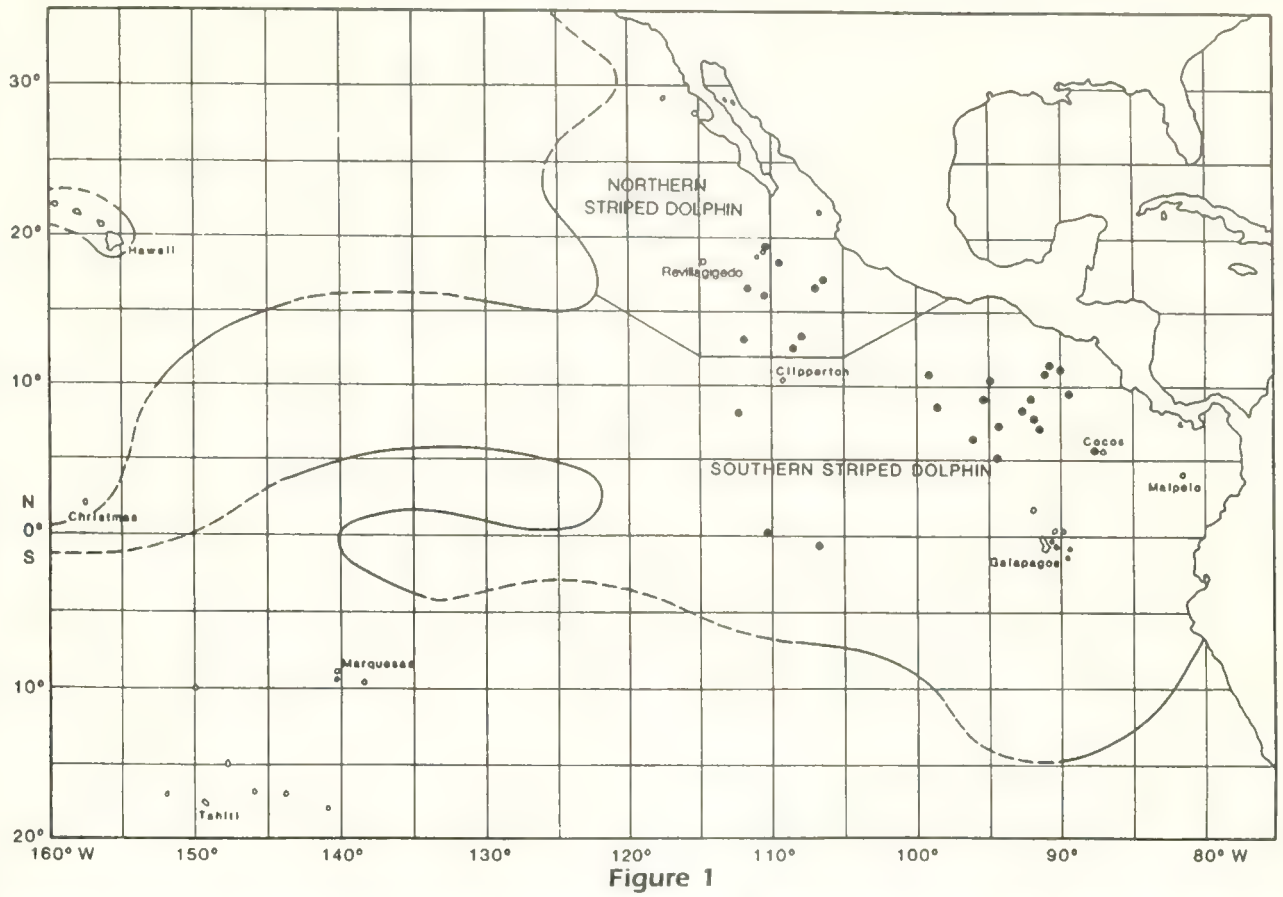

Figure 1

Distribution of schools of striped dolphin, *Stenella coeruleoalba*, (dark circles), from which data were taken for this report. Boundaries for northern and southern stocks were taken from Perrin et al. 1985.

camera mounted below the fuselage of a Hughes 500D helicopter that was launched from the NOAA Ship *David Starr Jordan*. This photographic sampling was part of a long-term research effort conducted by NMFS to monitor trends in abundance of dolphin populations in the ETP (Holt and Sexton, 1989; Wade and Gerrodette, in press).

The reconnaissance camera was equipped with a very fast, medium focal length lens (152 mm) and a forward image motion compensation system that eliminated the blur normally found in images taken from a low altitude, high-speed platform. We used Kodak Plus-X Aerecon II (thin-base) film, exposed through a medium yellow filter, throughout the experiment. This filter significantly reduced the amount of blue light reaching the film, thus enhancing both the contrast and resolution of our photographs.

The observer sitting in the right front seat of the helicopter triggered the camera, controlled cycle rate and shutter speed, and adjusted the forward motion compensation system. As each firing pulse was sent to the camera, a data acquisition system recorded the time that the image was captured and an altitude reading from the helicopter's radar altimeter. To check for accuracy in our recorded altitude data (A_r), we photographed calibration target arrays and compared altitude calculated from measurements of these known distances with recorded altitude (see Perryman and Lynn, 1993).

We found a consistent bias in A_r and used the linear regression equation shown below to calculate a corrected altitude (A_c) for each photograph used in this report.

$$A_c = (A_r)\ 1.013 - 33.755\ (r^2 = 0.993).$$

Length determination

We reviewed the images of 88 schools of striped dolphins photographed from 1987 through 1990 and selected the images of 28 schools that provided the best combination of image clarity and water penetration. From this sample, we selected the photographic pass over each school that captured the largest number of dolphins swimming parallel to and

very near the surface. Dolphins were not measured if either the rostrum or tail flukes were not clearly visible or if they were surfacing, diving, or jumping, which would make them appear shorter when viewed from above. Because there was from 80 to 90% overlap between adjacent photographs, the same dolphin could often be measured in two to four photographs. If more than one length was available for a dolphin, the largest length was selected, assuming it was the best determination of true length. This helped to minimize the reduction in apparent length caused by the normal swimming movements of the dolphins (Scott and Perryman, 1991; Perryman and Lynn, 1993).

We measured each dolphin from the tip of the rostrum to the trailing edge of the tail flukes (Fig. 2). These points were selected because the fluke notch that is used to determine standard length (Norris, 1961) was very difficult to see in most of the images. For adult specimens, this measurement should exceed standard length by 2–2.5 cm (Chivers, 1993[2]). The measurements were made on sections of the original black and white negatives that we captured with a high-resolution video camera and transferred to a Macintosh IIci computer. Image enhancement and length measurements were made with the aid of the digital image processing and analysis program, Image (version 1.37), which was developed by the National Institute of Health (W. Rasband, Research Services, Bethesda, Maryland). The length of each dolphin was determined by multiplying its length on the image by the scale of the photograph (scale= A_c/lens focal length).

Data analysis

Perrin et al. (1985) compared the mean lengths of physiologically adult male and female dolphins from putative geographic stocks of several species to provide supporting morphological evidence for reproductive isolation. For our analyses, we used length as the criteria for eliminating the youngest dolphins from our sample. Based on the length data for adult striped dolphins in Perrin et al. (1985) and a review of our length sample, we estimated that the minimum length for adult female striped dolphins in the eastern Pacific is about 180 cm. We used this length as our first cut-off point, and tested for differences (t-test) between the means of our length samples (≤180 cm) from the northern and southern regions (Fig. 1). Since the selection of this value was somewhat arbitrary, we repeated the tests on data sets with minimum values of 185 and 190 cm.

Based on behavioral arguments reviewed in Perryman and Lynn (1993), we assumed that the larger dolphin swimming closely alongside a calf was an adult female. Since this determination was based on behavior and not on examination of sexual characters, we qualify the term in quotation marks, "adult female," whenever we are referring to a length sample based on this assumption. A t-test was used to compare the mean lengths of "adult females" from the northern and southern regions. We also performed a power analysis to determine what range of differences between means we could expect to detect (probability of type II error ≤ 0.10) for this analysis and the ones described in the paragraph above.

Calf birth dates

We examined the length data from striped dolphins estimated to be one year old or less for evidence of pulses in reproduction (see Barlow [1984], for spotted and spinner dolphins; Perryman and Lynn [1993], for common dolphins). Ninety centimeters was used as the best estimate of average length at birth and 155 cm for average length at one year for striped dolphins in the eastern Pacific (Gurevich and Stewart, 1979[3]). We assumed postnatal growth was linear during the first year and back-projected the birth dates for all dolphins ≤155 cm in length. Our goal here was not to determine the ex-

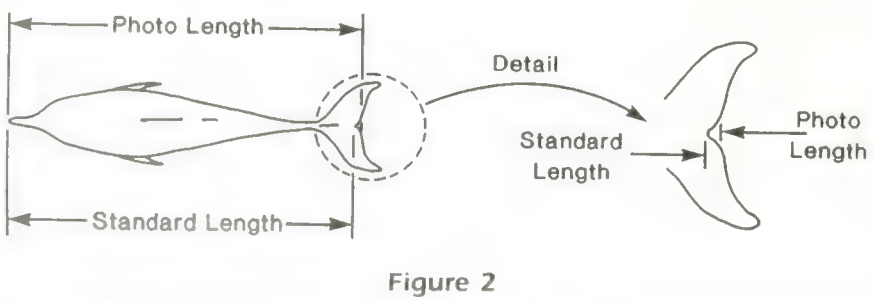

Figure 2

Illustration of the difference between points used to determine standard length and length as measured from our vertical photographs.

[2] S. Chivers. 1993. Southwest Fisheries Science Center, La Jolla, California 92037, unpubl. data.

[3] Gurevich, V. S., and B. S. Stewart. 1979. A study of growth and reproduction of the striped dolphin (*Stenella coeruleoalba*). U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Final Rep to NOAA, SWFC Contract 03-78-D27-1079, 29 p.

act date of birth for each dolphin but rather to examine the distribution of birth dates, based on the same assumptions, from the two regions. We used Kupier's modification of Kolmogorov's test for comparisons of circular distributions (Batschelet, 1965) to compare the calculated distribution of birth dates with a uniform distribution.

Comparisons with specimen data

We conducted four tests to compare the sample of photogrammetric lengths with data collected from striped dolphins killed incidentally in purse-seine fishing in the ETP (Perrin et al., 1976). The data from specimens included the information published by Perrin et al. (1985) and a small set of data from dolphins killed since 1985. *T*-tests were used to compare the mean length of "adult females" with the mean length of adult female specimens and with the mean length of lactating adult female specimens. We also compared the mean (*t*-test) and shape (Kolmogorov-Smirnov test) of the photogrammetrically determined length distribution of striped dolphins ≥ 180 cm with data from specimens ≥ 180 cm in length.

School structure

Examination of the structure of schools of striped dolphins captured in the drive fishery in Japan has revealed a distinct pattern of segregation based on sex, maturity, and length (Miyazaki, 1977, 1984; Miyazaki and Nishiwaki, 1978). Researchers have categorized these schools as adult, juvenile, or mixed depending on the proportion of juvenile dolphins (excluding calves) captured. In these studies, length (<174 cm) or age (<1.5 years) was used as the criterion for eliminating nursing calves from the sample; the remainder of the dolphins was determined to be juvenile or adult by direct examination of the gonads.

We examined the length distributions for the photographed schools to see if an analogous pattern of segregation in schools from the eastern Pacific was detectable. We divided our samples into two length categories which we labeled juvenile or adult. The minimum length for the juvenile category was set at 165 cm to eliminate nursing calves as described above. We selected this minimum value because 1) length at birth for striped dolphins from the ETP is apparently about 10 cm shorter than that reported from the western Pacific (Miyazaki, 1977; Gurevich and Stewart, 1979[3]), and we assumed that the difference in the average length at weaning was approximately the same; 2) dolphins larger than 165–170 cm in length were very rarely found swimming in the characteristic cow/calf configuration we see in our photographs.

We selected 195 cm as the upper bound for the juvenile category because this appears to be about the minimum size for adult male striped dolphins that have been killed in the ETP tuna purse-seine fishery (Perrin et al., 1985). This value was keyed to male length data because the studies of school structure from Japan indicated that a disproportionate number of the dolphins captured in juvenile schools were males (Miyazaki and Nishiwaki, 1978). Thus dolphins in each school were categorized as juvenile if they were between 165 and 195 cm in length and as adult if they were > 195 cm in length. The goal in this classification scheme was to create one category that would be composed of mostly juvenile and young adult dolphins and another that would include mostly adult animals.

We used chi-square analysis to test the hypothesis that the number of dolphins in the two categories in our schools was independent of school. For this analysis, we eliminated schools from which we had measured less than 20% of the school or fewer than 17 dolphins. The second criterion was established to minimize the number of predicted values in the chi-square analysis that were less than five. Application of these criteria reduced our sample to 21 schools for this test. Because the selection of 195 cm for the cut-off between the two size categories probably includes more adult females in the juvenile category than males, we decreased the limit to 190 cm and repeated the chi-square test. We also conducted a regression analysis to determine whether the proportion of the measured sample in the juvenile category was related to school size.

With the exception of the power analyses and birth date comparison which were done by hand, all tests presented in this report were performed with the program StatView developed by Abacus Concepts (Berkeley, CA). Unless noted otherwise, tests were considered significant for P values < 0.05.

Results

Regional comparisons

We compared the average length of striped dolphins from the northern and southern regions and found no significant differences between the samples (Table 1; Fig. 3). In tests for differences in mean lengths of "adult females" (Fig. 4), no differences were found between the regions. Although none of the differences was significant, means of the

samples from the northern region were generally a few centimeters smaller than those from the south, a pattern reported by Perrin et al. (1985). This level of difference was less than we could detect given the available sample and the variability of our data (Table 2). With this length sample, it appears that we can expect to detect differences between means that differ by at least 4 cm.

Table 1

Results of *t*-tests for differences between means of length samples from striped dolhin, *Stenella coerueoalba*, from the northern (Nor) and southern (So) regions.

Sub-sample (cm)	*n* Nor/So	mean (cm) Nor/So	*P* (2-tailed)
>180	160/251	205.1/205.9	0.476
>185	154/484	206.0./207.7	0.138
>190	140/450	207.9/209.2	0.230
"Adult females"	19/63	200.2/204.0	0.201

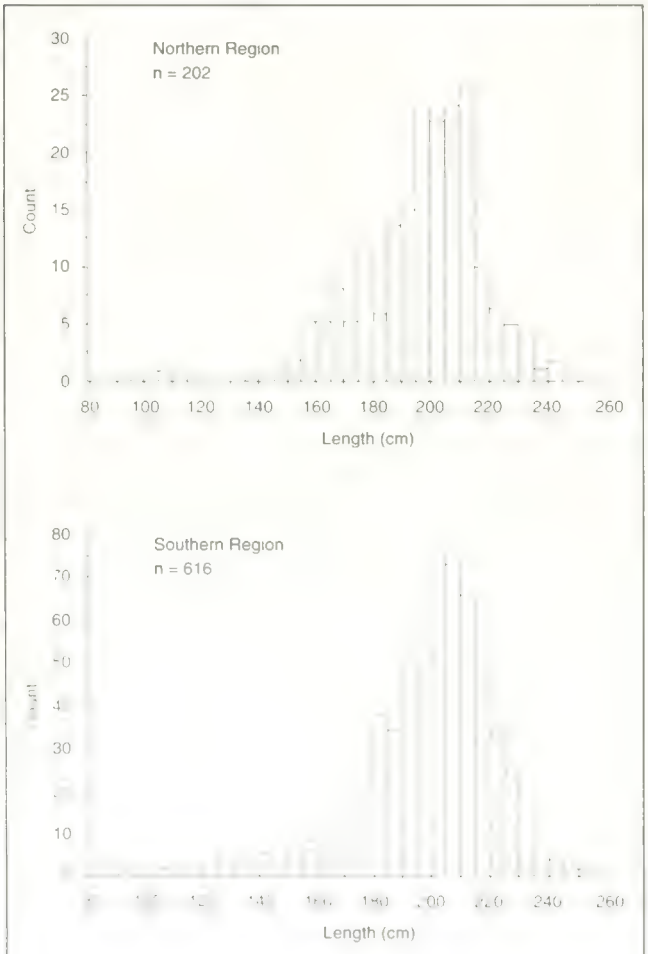

Figure 3

Distribution of lengths of striped dolphins, *Stella coeruleoalba*, measured from the northern and southern regions.

Table 2

Minimum detectable differences between means for *t*-tests for samples from striped dolphins, *Stenella coerureoalba*, from the northern (Nor) and Southern (So) regions. Beta error set at 0.10.

Variance Sub-sample (cm)	Nor/So	*t*-value	Minimum detectable difference (cm)
>180	164.99 190.11	1.963	4.01
>185	148.23 162.59	1.964	3.82
>190	122.21 141.94	1.964	3.72
"Adult females"	53.61 147.57	1.292	9.63

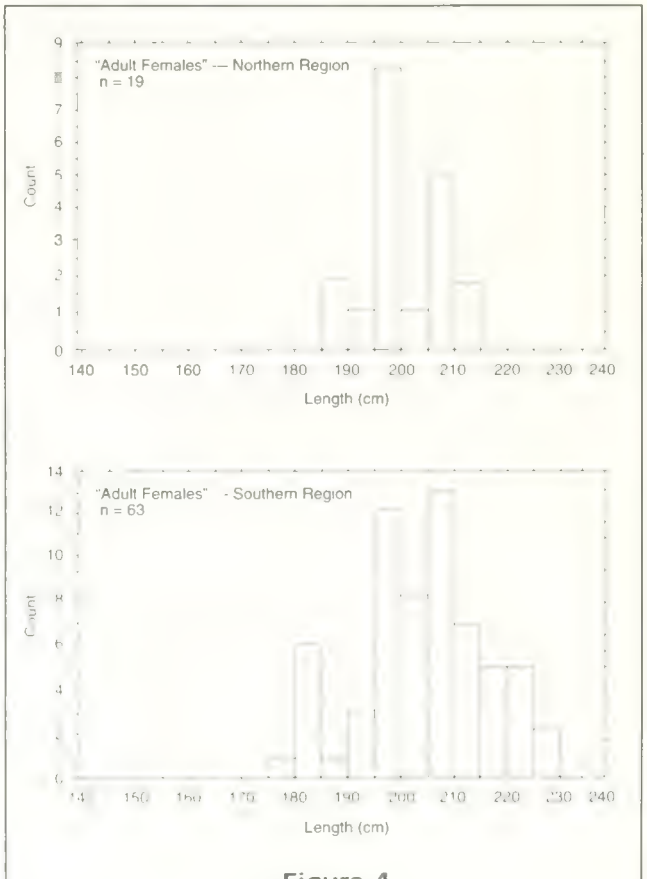

Figure 4

Distribution of lengths of "adult females", defined here as stroped dolphins, *Stenella coeruleoalba*, closely associated with a calf, measured from the northern and southern regions.

The sample from the northern region was too small to test for a seasonal pattern in reproduction, but the distribution of back-projected births from the southern region differed significantly from the uniform distribution ($P<0.01$; Figs. 5 and 6). Reproduction for striped dolphins from the southern region appears to be broadly pulsed in the fall through spring period.

Photogrammetric and specimen data

Since significant differences between length samples from the northern and southern regions could not be detected, we pooled length data from the two regions in the tests that follow. We found that "adult females" were significantly longer (4.8 cm) on average than adult females from the specimen data base. When the test was repeated by using length data for lactating females from the specimen data base, the two samples no longer differed significantly (Table 3). Striped dolphins ≥ 180 cm in length from the photogrammetric sample were significantly longer on average than the sample based on the same length criteria from specimen data. We also performed a Kolmogorov-Smironov test to compare the two distributions (Fig. 7) and found that they differed significantly ($P<0.01$).

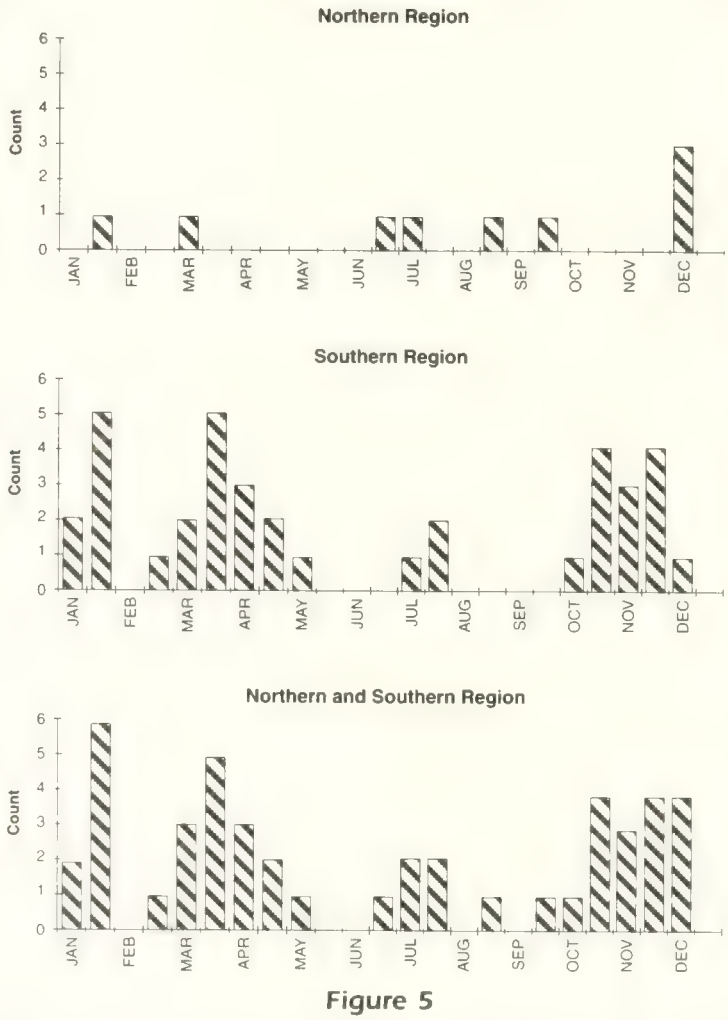

Figure 5

Distribution of back-projected birth dates for striped dolphins, *Stenella coeruleoalba,* from the northern and southern regions and for the two regions combined.

Table 3

Results of comparisons between means of length data for striped dolphins, *Stenella coerueoalba,* taken from specimens (spec) and aerial photographs (photo) (*t*-tests), and the distribution of lengths ≥180cm (Kolmogorov-Smirnov {*k* and *s*} test) from these two sources.

Comparison	*n* spec/photo	Mean (cm) spec/photo	*P* (2-tailed)
Adult females specimen/photo	50/82	198.2/203.0	0.007
Lactating specimens/ "adult females"	23/82	199.8.203.0	0.202
>180cm *t*-test	256/681	199.19/205.73	0.0001
>180cm *k* and *s*	256/681	Z=3.378	0.0007

School size and structure

We performed a chi-square test to determine whether the number of dolphins in our two size categories were distributed randomly between schools (Fig. 8) and the hypothesis was significantly rejected when the maximum length for the juvenile category was 195 or 190 cm ($P<0.001$). With a maximum value of 190 cm, four expected values generated by the test were lower than five. When these schools were deleted from the test or lumped with adjacent schools to eliminate these low expected values, the test results remained highly significant.

When school size was regressed against proportion in the juvenile category, the slope of the regression was not significantly different from zero. Thus, in our sample, the proportion of small dolphins in a school was not related to school size.

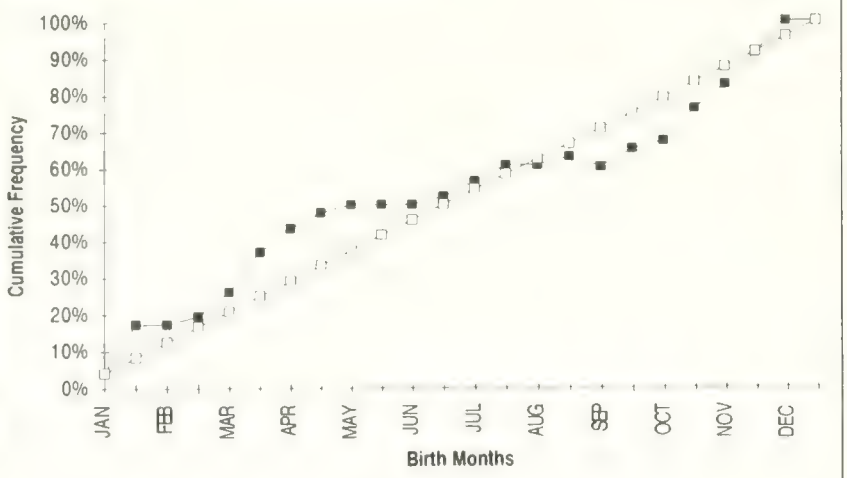

Figure 6

Cumulative distribution of back-projected striped dolphin, *Stenella coeruleoalba,* birth dates (solid squares) and those predicted by a uniform distribution of births (open squares).

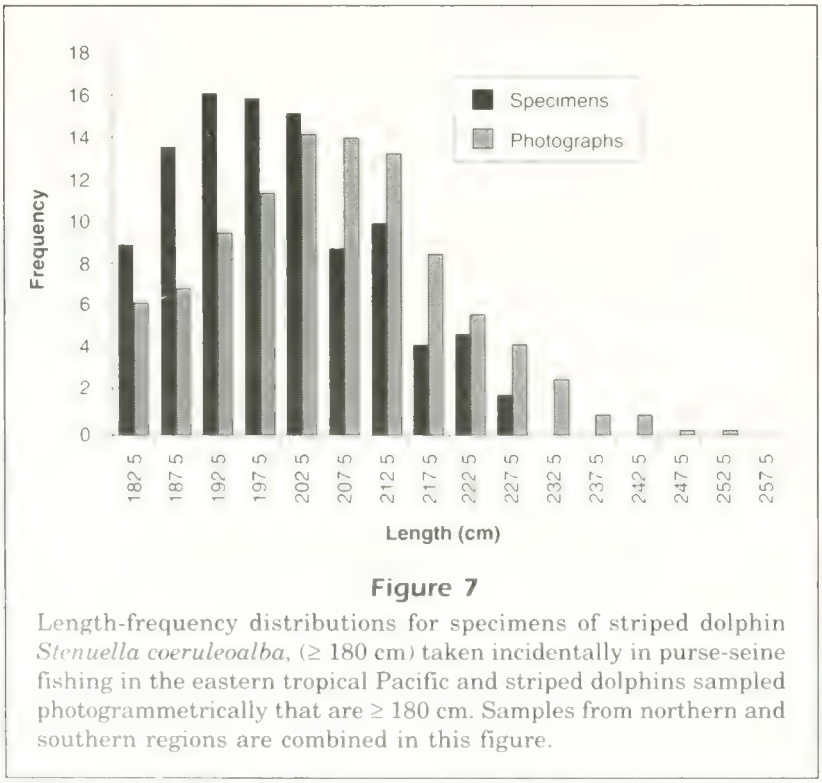

Figure 7

Length-frequency distributions for specimens of striped dolphin *Stenuella coeruleoalba,* (≥ 180 cm) taken incidentally in purse-seine fishing in the eastern tropical Pacific and striped dolphins sampled photogrammetrically that are ≥ 180 cm. Samples from northern and southern regions are combined in this figure.

Discussion

We found no significant differences in our length samples of striped dolphins from the northern and southern regions to support a recommendation that they be managed as separate stocks. This must be tempered by the fact that length differences of a scale not detectable in our sample, i.e. < 4 cm, could exist. The case for two stocks is also weakened by the distribution of sightings of this species from recent research vessel surveys (Wade and Gerrodette, in press). These data indicate that, although a hiatus in striped dolphin distribution exists in the typically tropical (high temperature, low salinity) inshore habitat centered around lat. 15° N, there appears to be a broad avenue for movement between the northern and southern regions in the upwelling modified habitat east of long. 110° West (Au and Perryman, 1985; Reilly, 1990).

When we compared our sample of lengths for "adult females" and dolphins ≥ 180 cm with data from specimens killed incidentally in purse-seine fishing, we found that the means from the photogrammetric sample were significantly larger (by about 3–6 cm). This does not seem unreasonable at first glance because our measurements to the trailing edge of the flukes rather than to the fluke notch introduces a positive bias in the photogrammetric data of about 2–2.5 cm. Also, the "adult female" category probably includes only those females who have carried and given birth to a live calf, thus eliminating the younger, presumably smaller, females who are physiologically adult but have not yet had a successful pregnancy. However, these results for adult females are contrary to previous comparisons of photographic and specimen data for northern and central common dolphins (Perryman and Lynn, 1993) and eastern spinner dolphins (Perryman, unpubl. data). Since the photogrammetric data for all of these taxa were collected in the same manner, it seems likely that the difference between the two striped dolphin samples reflects some form of selectivity in either or both sampling systems.

The schools of striped dolphins that we photographed showed a pattern of segregation by length

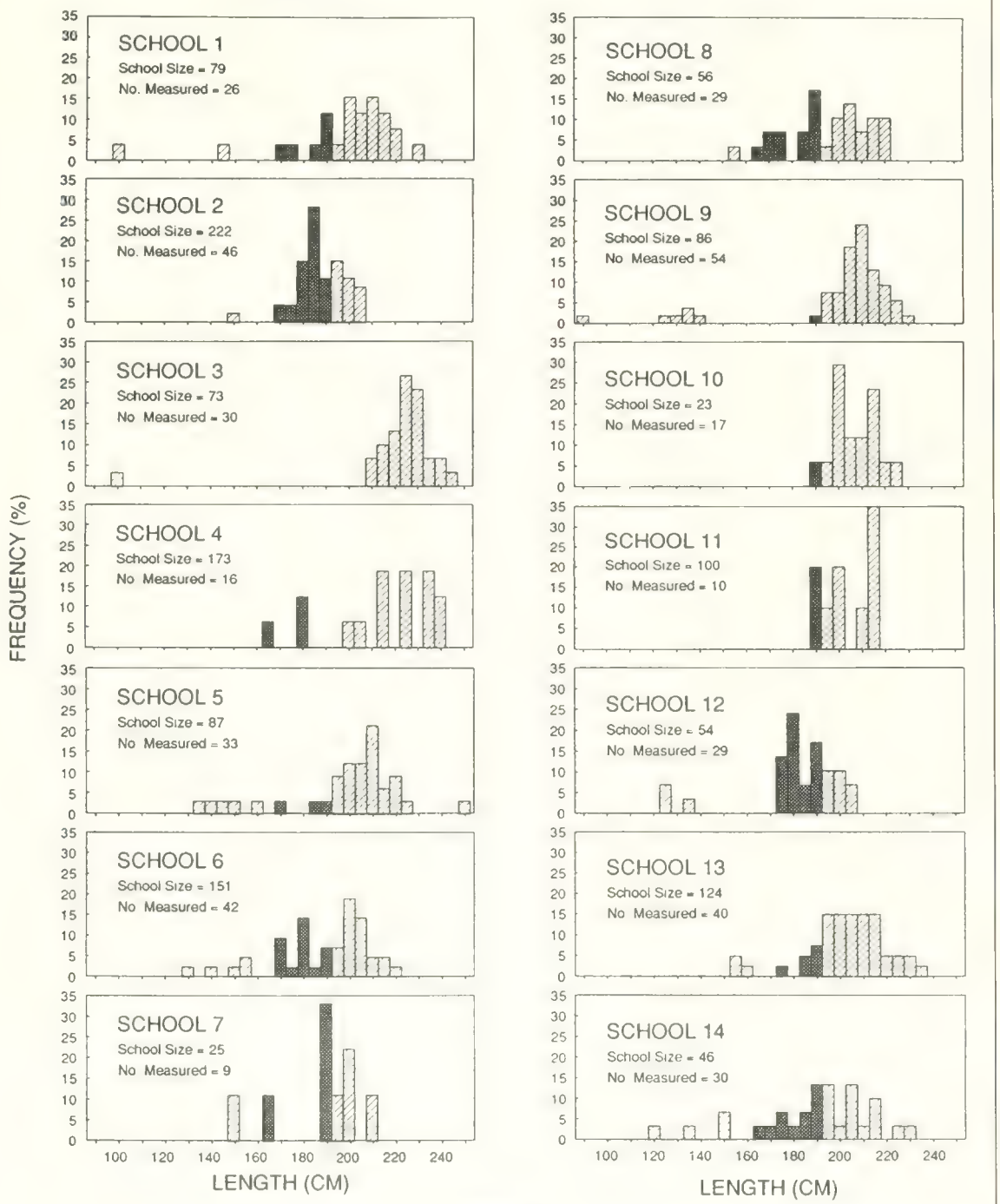

Figure 8

Length frequencies for each school of striped dolphins, *Stenella coeruleoalba*. Shaded bars indi cated lengths of dolphins that were included in the juvenile categeory.

that is very similar to that reported from the western Pacific (Miyazaki, 1977; Miyazaki and Nishiwaki, 1978). It also appears that the proportion of smaller dolphins in our sample of schools is not related to school size. Possibly this segregation is the explanation for differences between specimen and photogrammetric data sets.

Tuna fishermen select dolphin schools for encirclement based mainly on the amount of tuna associated with the school. Schools of younger/smaller

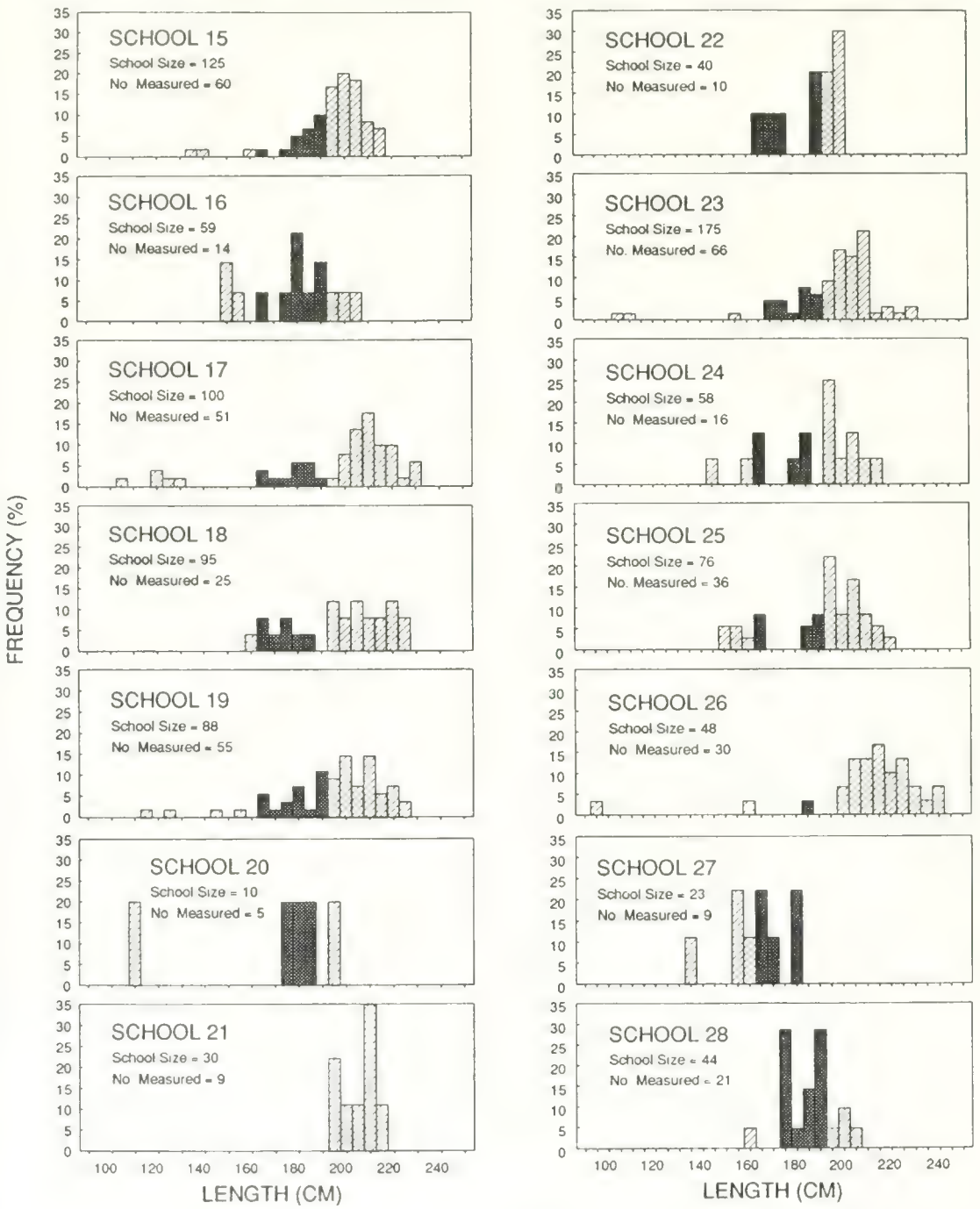

Figure 8 (Continued)

striped dolphins might carry more tuna and be captured more frequently than schools composed of adult animals. If the bond between yellowfin tuna and dolphins is related to size and hydrodynamics as suggested by Edwards (1992) then it may be that the smaller striped dolphins are hydrodynamically more suitable for this association. Juvenile schools of striped dolphins are made up of animals that are about the same length as schools of spotted or spinner dolphins for which the tuna-dolphin association appears to be the strongest.

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Literature cited

Au, D. W. K., and W. L. Perryman.
1985. Dolphin habitats in the eastern tropical Pacific. Fish. Bull. 83:623–643.

Batschelet, E.
1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. Am. Inst. Biol. Sci. Monograph, 57 p.

Barlow, J.
1984. Reproductive seasonality in pelagic dolphins (*Stenella* spp.): implications for measuring rates. Rep. Int. Whaling Comm. Spec. Issue 6:191–198.

DeMaster, D. P., E. F. Edwards, P. Wade, and J. E. Sisson.
1992. Status of dolphin stocks in the eastern tropical Pacific. *In* D. R. McCullough and R. H. Barrett (eds.), Wildlife 2001: populations. p.1038–1050. Elsevier Science Publs., New York.

Dizon, A. E., W. F. Perrin, and P. A. Akin.
In press. Stocks of dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific: a phylogeographic classification. NOAA Tech. Rep.

Edwards, E. F.
1992. Energetics of associated tunas and dolphins in the eastern tropical Pacific Ocean: a basis for the bond. Fish. Bull. 90:678–690.

Holt, R. S., and J. E. Powers.
1982. Abundance estimation of dolphin stocks in the eastern tropical Pacific yellowfin tuna fishery determined from aerial and ship surveys to 1979. NOAA Tech. Mem. NMFS SWFSC 23, 95 p.

Holt, R. S., and S. N. Sexton.
1989. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1986 data, the first year. Fish. Bull. 88:105–111.

Miyazaki, N.
1977. School structure of *Stenella coeruleoalba*. Rep. Int. Whaling Comm. 27:498–499.
1984. Further analysis of reproduction in the striped dolphin, *Stenella coerueoalba*, off the Pacific coast of Japan. Rep. Int. Whaling Comm. Spec. Issue 6:343–353.

Miyazaki, N., and M. Nishiwaki.
1978. School structure of the striped dolphin off the Pacific Coast of Japan. Scientific Reports of the Whales Research Institute. 30:65–115.

Norris K. S. (ed.)
1961. Standardized methods for measuring and recording data on smaller cetaceans. J. Mammal. 42:471–476.

Perrin, W. F., J. M. Coe, and J. R. Zweifel.
1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull. 74:229–269.

Perrin, W. F., M. D. Scott, G. J. Walker, and V. L. Cass.
1985. Review of the geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. NOAA Tech. Rep. NMFS 28. 28 p.

Perryman, W. L, and M. Lynn.
1993. Identification of geographic forms of common dolphin (*Delphinus delphis*) from aerial photogrammetry. Mar. Mammal Sci. 9:119–137.

Reilly, S. B.
1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Mar. Ecol. Prog. Ser. 66:1–11.

Scott, M. D., and W. L. Perryman.
1991. Using aerial photogrammetry to study dolphin school structure. *In* K. Pryor and K. S. Norris, (eds.), Dolphin societies-discoveries and puzzles, p. 227–241. Univ. California Press, Berkeley.

Wade, P. R., and T. Gerrodette.
In press. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. Rep. Int. Whaling Comm. 43.

Potential tuna catches in the eastern Pacific Ocean from schools not associated with dolphins

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Abstract.—The eastern Pacific purse-seine tuna fishery has historically been very productive, yielding up to 400,000 metric tons (t) per year of primarily yellowfin, *Thunnus albacares*, and skipjack, *Katsuwonus pelamis*. However, efforts to minimize dolphin (primarily spotted dolphin, *Stenella attenuata*, spinner dolphin, *S. longirostris*, and common dolphin, *Delphinus delphis*) mortality incidental to tuna seining in the eastern Pacific ocean have been increasing. Therefore, predictions of what the tuna catches will be in the future, if there is a ban or moratorium on catching dolphin-associated tuna, are useful. Based on recruitment levels, age-specific catchability coefficients for yellowfin tuna caught without dolphins, and average fishing effort observed during 1980-88, we predicted that yellowfin catches would be reduced by an average of about 25%. These results were verified by Monte Carlo simulations, by using average effort and randomly selected yellowfin recruitment and catchability coefficients from 1980 to 1988, which predicted a mean annual decrease of 55,563 t or 24.7% of yellowfin catch. The actual reduction in yellowfin catch might be greater because 1) fishing effort will probably decline, 2) the range of the fishery might be reduced to the traditional inshore non-dolphin regions, and 3) yellowfin recruitment could be reduced by the change in age structure and population size likely to result from a moratorium. Because skipjack seldom associate with dolphins, redirection of fishing effort to schools of tuna not associated with dolphins would probably result in increased skipjack catch rates. However, the magnitude of the increase is difficult to estimate, because the population dynamics of skipjack are poorly understood. Finally, this study predicted that the catches in the first years after a moratorium on dolphin sets would not necessarily reflect long-term catches.

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Since the late 1950's, purse-seine fishermen in the eastern Pacific Ocean (EPO), knowing that schools of yellowfin tuna (*Thunnus albacares*) often associate with dolphins (primarily spotted dolphins, *Stenella attenuata*, spinner dolphins, *S. longirostris*, and common dolphins, *Delphinus delphis*), have used the dolphins to help locate and capture yellowfin. Dolphins are relatively easy to detect, being larger and closer to the surface than yellowfin. In fact, the most efficient means of catching the 2- and 3-year-old yellowfin, which comprise the largest component of the tuna catch in the EPO, is purse-seine fishing for dolphin associated schools (Punsly and Deriso, 1991). Yellowfin remain associated with dolphins while the net is being set around the dolphin herds. The fishermen attempt to release all of the dolphins from the net; however, incidental mortality sometimes occurs through entanglement.

As a result of increasing public pressure to prevent mortality of dolphins incidental to tuna purse seining, elimination of setting on dolphin-associated tunas is being considered. Therefore, fishermen, biologists, and managers need to know the extent to which tuna catch in the EPO might be reduced by the elimination of sets on dolphin-associated fish. The objective of this study was to estimate this potential reduction in the catch. No such estimates have been published previously.

Tuna catches could be affected by a ban or moratorium on dolphin sets in six ways:

1 The overall catchability of yellowfin by purse seiners could be reduced.
2 The yield per recruit of yellowfin could decline because non-dolphin-associated yellowfin caught by purse seiners are mostly composed of fish younger than the optimum age of entry (Calkins, 1965; Allen, 1981).
3 The average age of yellowfin and mean biomass may be reduced by fishing on younger age groups. This might not only reduce the catch in weight, but also reduce the spawning potential and possibly the resulting recruitment.
4 Since the offshore EPO purse-seine fishery is directed primarily at dolphin-associated fish (Fig. 1, A and B), a moratorium on setting on dolphin herds could result in a contraction of the range of the fishery into inshore regions. The number of fish recruited to this new smaller area might be lower than the number recruited to the entire area. Lower effective recruitment would also result in lower catches.
5 If a moratorium on catching dolphin-associated tuna occurs,

some purse-seine fishermen may decide to move to other oceans or retire, which would reduce total fishing effort and hence the catch.

6 Since skipjack tuna (*Katsuwonus pelamis*), the only other primary target species in the fishery, seldom associate with dolphins, their catch may increase if effort remains at 1980–88 levels and is directed only toward tuna schools not associated with dolphins.

Because no relation between spawners and recruitment of yellowfin has been established (Bayliff, 1992, p. 62), the possible effects of reduced recruitment were not addressed in this study. Also, since the authors cannot predict how many seiners would leave the EPO, or how much the fishery would contract, these two factors were not considered. In other words, this study only attempted to estimate how much tuna catches might change due to changes in yellowfin catchability, yield per recruit, total biomass, and age structure.

To measure the possible effects of changing the mode of fishing from being directed toward primarily dolphin-associated schools of tuna ("dolphin sets," Allen, 1981) to one directed at exclusively free-swimming schools ("school sets") and floating-object-associated schools ("log sets," Greenblatt, 1979), we first estimated what the tuna catches would have been in previous years if dolphin sets had been replaced by non-dolphin sets. Then the estimates were compared with actual catches. Our method used non-dolphin-set catchability coefficients and total effort to estimate what the catches would have been during 1980–88 if there had been a moratorium on dolphin sets beginning in 1980. Other works in which catches were estimated for alter-

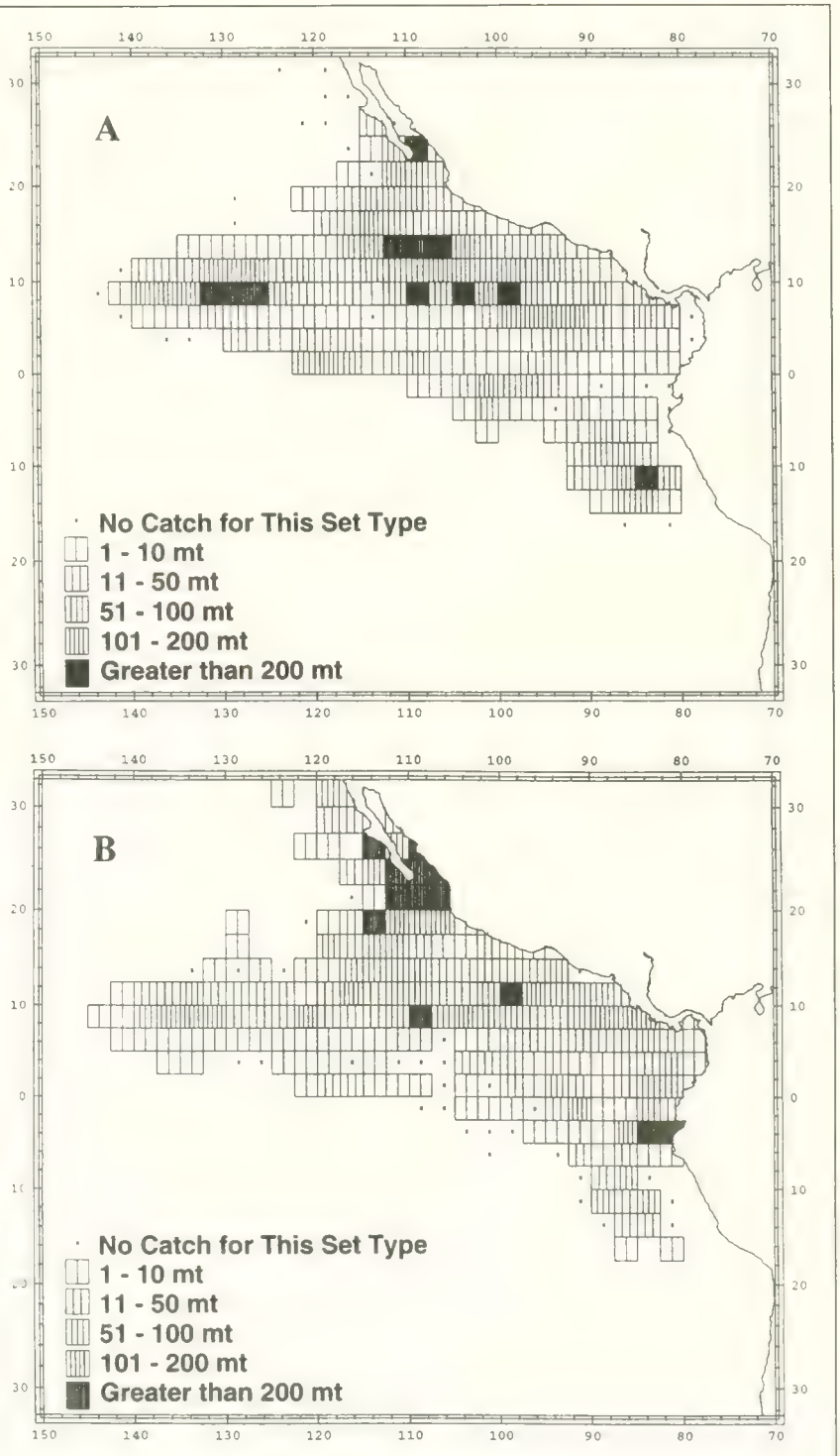

Figure 1

(**A**) Geographic distribution of average yellowfin tuna (*Thunnus albacares*) catch by purse seiners, during 1980–88, from schools associated with dolphins (Delphinidae). Catches are expressed in metric tons by 2.5–degree quadrangles. (**B**) Geographic distribution of average yellowfin catch by purse seiners, during 1980–88, from schools not associated with dolphins. Catches are expressed in metric tons by 2.5–degree quadrangles.

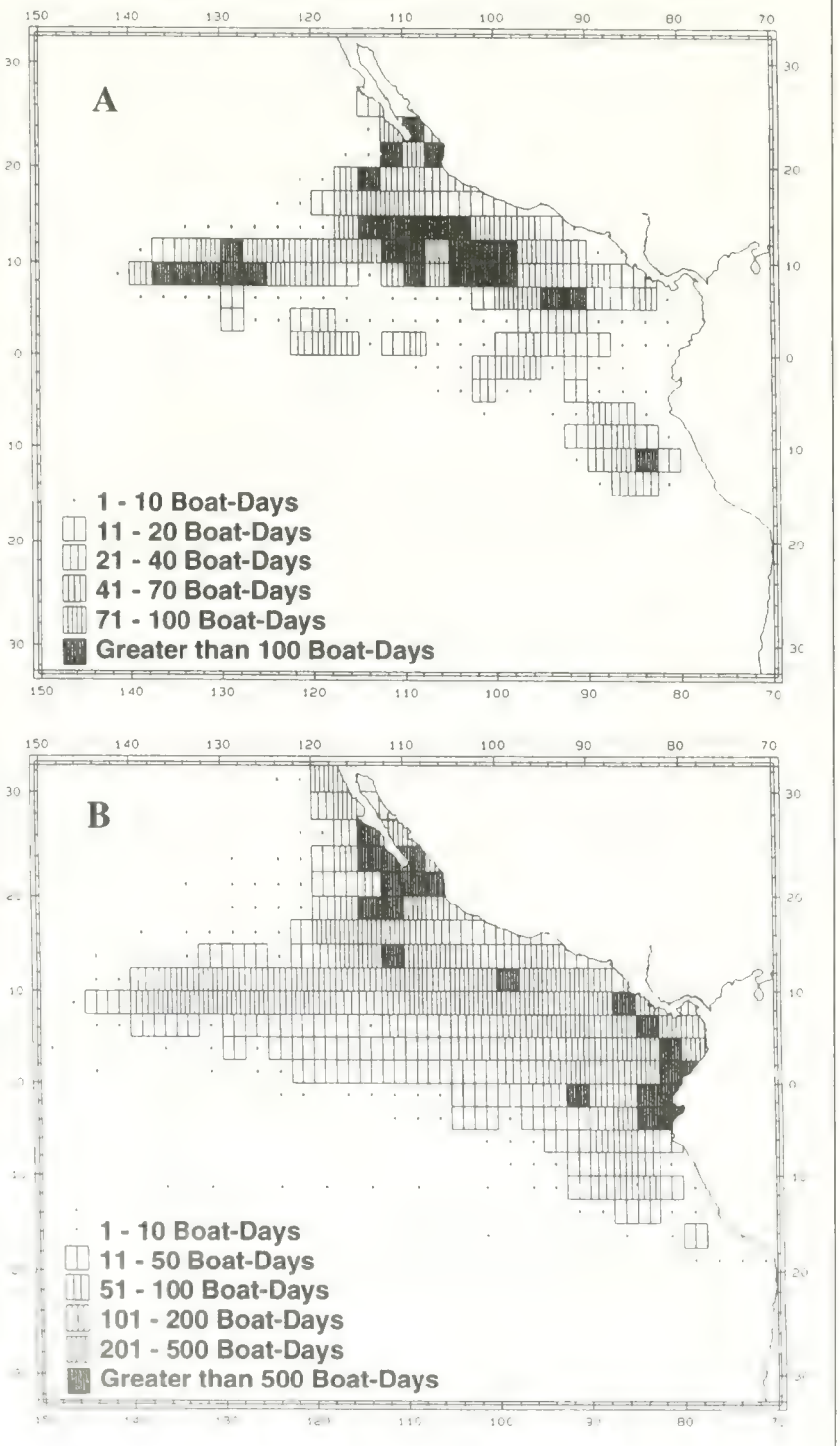

Figure 2

(**A**) Geographic distribution of total purse-seiner fishing effort during 1980–88 which lead to dolphin (Delphinidae) sets. Effort levels are expressed in boat-days of fishing by 2.5–degree quadrangles. (**B**) Geographic distribution of total purse-seiner fishing effort during 1980–88 which lead to non-dolphin sets. Effort levels are expressed in boat-days of fishing by 2.5–degree quadrangles.

native catchability coefficients include Holt (1958), Jones (1961), and Bartoo and Coan (1978).

Materials and methods

Data

The Inter-American Tropical Tuna Commission's (IATTC) logbook and length-frequency data bases were used in this study. The logbook data base, described in Orange and Calkins (1981), Punsly (1983; with emphasis on set types), and Punsly (1987; with emphasis on yellowfin catch rates), contains information on the fishing activities of about 90% of the purse seiners in the EPO. Total catches were estimated by multiplying the logbook catches by the ratio of the sum of the unloading weights to the sum of the logbook catches. Geographic distributions of the logbook data on catch and effort, during 1980–88, for both dolphin-associated and unassociated schools are shown in Figures 1 and 2. The length-frequency data base, described by Hennemuth (1957), Punsly and Deriso (1991), and Tomlinson et al. (1992), has information from samples of about 12–15% of the catch. Age-specific yellowfin abundances from cohort analysis (Pope, 1972; also called sequential computation of stock size in Ricker, 1975; and virtual population analysis in Gulland, 1965) were taken from Bayliff (1990).

Data from 1980 to 1988 were used in this study. Data before 1980 were not used because of the difficulty in modeling the closed seasons for yellowfin (Cole, 1980). Data after 1988 were not used because cohort analysis cannot produce accurate abundance estimates for cohorts which have not been in the fishery for a sufficient period of time.

Semi-annual age groups used in this study were described in detail

in Bayliff (1992, p. 52). Monthly age compositions were estimated by combining 1-cm length-interval data into semi-annual age groups by fitting multinormal distributions to the data with the aid of the computer program NORMSEP, (Abramson, 1971), and constraining the fit to the growth parameters of Wild (1986). "X" and "Y" cohorts were defined as those fish reaching 30 cm, which correspond to the approximate age of first recruitment, during the fourth and second quarters of the year, respectively. Age groups in our study, 0.5 to 5.5 in 0.5 year increments, correspond to the Y0, X1, Y1 ... Y5 cohorts, respectively, in Table 21 of Bayliff (1992).

Estimates of fishing effort

The total monthly effort by purse seiners was estimated as

$$\hat{E}_{om} = f_{om} Y_{om} / y_{om},$$

where o, refers to the observed mixture of set types, Y_{om} is the yellowfin catch unloaded by purse seiners in month (m), y_{om} is the yellowfin catch reported in the IATTC logbooks and f_{om} is the effort, in boat-days of fishing, reported in the logbooks. Effort on non-dolphin sets for all purse seiners was estimated by

$$\hat{E}_{nm} = \sum_{cs} \sum \hat{f}_{nmcs} Y_{omcs} / \hat{y}_{omcs},$$

where $\hat{f}_{nmcs}$ is the fishing effort which lead to non-dolphin (n) sets by monitored vessels of size (s) from country (c), Y_{omcs} is the total catch of yellowfin from unloadings by size (s) vessels from country (c), and $\hat{y}_{omcs}$ is the total yellowfin catch by monitored vessels. These estimates were stratified by country and size of vessel because the proportion of dolphin sets is affected by these two factors.

Estimates of skipjack catches if all effort were non-dolphin

Skipjack are suspected to be mostly transient in the EPO (Joseph and Calkins, 1969), so we assumed that depletion is probably unimportant. Thus, the ratio of the total effort to the non-dolphin effort was used to estimate skipjack catches:

$$\hat{Y}_{pm}(SJ) = Y_{nm}(SJ) \hat{E}_{om} / \hat{E}_{nm},$$

where $\hat{Y}_{pm}(SJ)$ is the potential (p) non-dolphin, skipjack catch and $Y_{nm}(SJ)$ is the actual non-dolphin-set, skipjack catch. In essence, skipjack catches were estimated to be linear extrapolations of catch rates to higher levels of effort.

Estimation of yellowfin catches if all effort were non-dolphin

This method used age-specific, monthly catchability coefficients by fishing mode and allowed the future population structure to be affected by previous catches. First, age-specific catchability coefficients for non- dolphin sets (n) in each month (m) were estimated for each semi-annual age group (j):

$$\hat{q}_{nmj} = \hat{C}_{nmj} / \left(\hat{E}_{nm} \overline{N}_{mj} \right),$$

where $\hat{C}_{nmj}$ are the monthly, total, non-dolphin purse-seine catches (in numbers of fish) of semi-annual age group (j) and $\overline{N}_{mj}$ are the age-specific, monthly, average abundances estimated by the cohort analysis (Bayliff, 1990). Beginning with the population structure in January 1980, obtained from cohort analysis, we estimated what the catch in each month of each semi-annual age group would have been without dolphin sets; i.e.,

$$\hat{C}_{pmj} = \left[\left(\hat{N}_{mj} \hat{q}_{nmj} \hat{E}_{om} \right) / \left(\hat{q}_{nmj} \hat{E}_{om} + \overline{M}_j \right) \right] \left[1 - e^{-\left(\hat{q}_{nmj} \hat{E}_{om} + \overline{M}_j \right)} \right],$$

where $\overline{Mj}$ is the age-specific, instantaneous, monthly natural mortality (Bayliff, 1992, p. 52). Yield in weight was estimated by

$$\hat{Y}_{pmj} = \overline{W}_m(j) \hat{C}_{pmj},$$

where $\overline{W}(j)$ is the estimated mean weight of age (j) yellowfin in month m caught during 1980–88. The subsequent month's abundance of semi-annual age group (j) was estimated to be

$$\hat{N}_{m+1,j} = N_{mj} e^{-\left(\hat{q}_{nmj} \hat{E}_{om} + \overline{M}_j \right)},$$

except for the months of recruitment (May and January), when $\hat{N}_{JAN,2}$ and $\hat{N}_{MAY,3}$ were set equal to the historical recruitment previously estimated for that time period by cohort analysis. Yellowfin form the first semi-annual age group (those fish hatched in the middle of the current year) were not included in the analysis because they were not recruited until the next year, when they became semi-annual age group 3. Each January, the semi-annual age groups were graduated as follows:

$$\hat{N}_{JAN,j+2} = N_{DEC,j} e^{-\left(\hat{q}_{nmj} \hat{E}_{om} + \overline{M}_j \right)}.$$

Monte Carlo simulation

The age-structure method produced catches specific to the observed time-series of recruitment and age-specific catchability coefficients during 1980– 88. Additional information can be gained by estimating what the trend in catches would be if the recruitment and catchability trends were different. In order to explore the range of resulting catches which might have occurred under various conditions, a Monte Carlo simulation was used. Paired simulations were performed for both the observed mixed-mode fishery and a fishery in which all effort was directed toward non-dolphin-associated tuna. Frequency distributions of differences between catches from the two simulated fisheries provide a more comprehensive estimate of future expectations.

The simulations used quarterly time steps and 1,000 replicates. At each quarter of each year in each replicate, a year between 1980 and 1988 was randomly selected with replacement (i.e., each year could be selected more than once). Pairs of quarterly catchability coefficients (one from the observed mixture of fishing modes and one for the non-dolphin sets only) estimated for the corresponding year, were used in the calculations during the time steps. Quarterly coefficients were calculated with the same equation as that for the monthly coefficients with months replaced by quarters. Quarterly fishing efforts were set to the 1980–88 averages. The same average total effort was applied to both the observed and non-dolphin fishing-mode models.

Recruitment was simulated to occur in the second and fourth quarter. For each year in each simulation, a randomly selected year was chosen. Recruitment pairs (X and Y) from the randomly selected year were used for both fishery models. Initial population sizes and age structures were also set to the 1980–88 averages.

One thousand differences between the simulated catches for the mixed- mode and non-dolphin only scenarios were generated for a time series of nine years. The 95% confidence intervals corresponded to the 50th and 950th highest differences from the 1,000 simulations. Because yellowfin usually live for less than 5 years (Fig. 3), results for the last (9th) year were unaffected by the initial age structure.

Results

Deterministic approach

If trends in total effort, recruitment, and non-dolphin-set catchability coefficients had been the same as during 1980–88, with all effort directed at non-dolphin sets, yellowfin catches (Table 1, column NYF) were estimated to have averaged 77% of the observed catch (Table 1, column OYF). The range was from 58% in 1985 when dolphin-associated tuna fishing was good to 93% in 1983 when dolphin-associated tuna fishing was poor. The reasons why the ratio of estimated catch without dolphin sets to the observed catch varied annually can be seen in Figures 3–7. For example, the high estimated biomasses of 1.5-year-old yellowfin in 1988 (Fig. 4), coupled with their high non-dolphin-set catchability coefficients (Fig. 5), produced an estimated catch of 266,000 t for all effort directed at non-dolphin sets, which was almost as high as the 303,000 t catch estimated from the catchability coefficients for the observed mixture of set types (Fig. 6). Catchabilities could have increased in 1988 for a variety of reasons, including the use of deeper nets, the use of "bird radar" (relatively new radar used for detecting birds which commonly have tuna beneath them) or environmental factors, such as a shoaling of the thermocline (Green, 1967). For a given level of effort, catches depended on the age-specific abundances (Figs. 3 and 4) and catchability coefficients (Figs. 5 and 6). Consequently, the estimated catches if all effort were directed at non-dolphin sets approached

Table 1

Estimated annual tuna (Scombridae) catches by purse seiners in the eastern Pacific ocean, in thousands of metric tons.

Year	OYF	NYF	QYF	OSJ	NSJ	OT	QT	NT
1980	170	129	158	131	155	301	313	284
1981	190	152	146	120	151	310	297	303
1982	134	111	120	99	129	233	249	240
1983	104	96	98	58	73	162	171	169
1984	155	103	125	61	90	215	215	193
1985	227	132	169	49	99	276	268	231
1986	286	193	168	64	113	350	281	305
1987	285	243	195	62	120	347	314	363
1988	303	266	229	85	123	388	352	389
Mean	206	158	156	81	117	286	274	275

OYF = yellowfin tuna (*Thunnus albacares*) - observed mixture of set types.
NYF = yellowfin tuna - all effort directed at non-dolphin (Delphinidae) sets, using the observed monthly catchability coefficients for non-dolphin sets.
QYF = yellowfin tuna - all effort directed at non-dolphin sets, using the average, observed, quarterly catchability coefficients for non-dolphin sets.
OSJ = skipjack tuna (*Katsuwonus pelamis*) - observed mixture of set types.
NSJ = skipjack tuna - all effort directed at non-dolphin sets.
OT = yellowfin plus skipjack tuna - observed mixture of set types.
QT = yellowfin plus skipjack tuna - effort directed at non-dolphin sets, using quarterly average catchability coefficients.
NT = yellowfin plus skipjack tuna - all effort directed at non-dolphin sets, using monthly catchability coefficients.

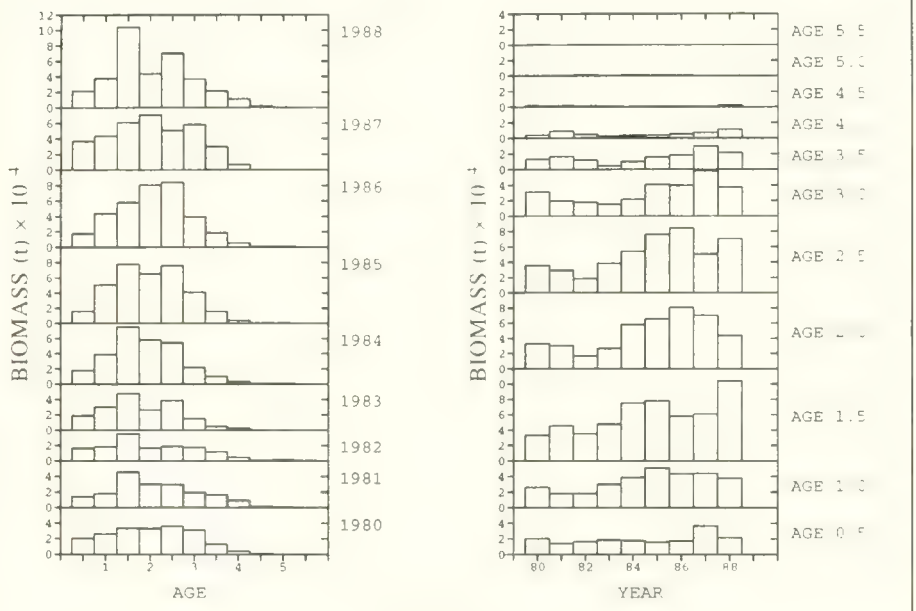

Figure 3

Estimated average annual biomasses (t) of yellowfin tuna (*Thunnus albacares*) by semi-annual age group for the observed mixture of set types. In the left panel, biomasses are summarized by age within year. In the right panel, biomasses are summarized by year within age group. Age refers to the age in years at the middle of the year.

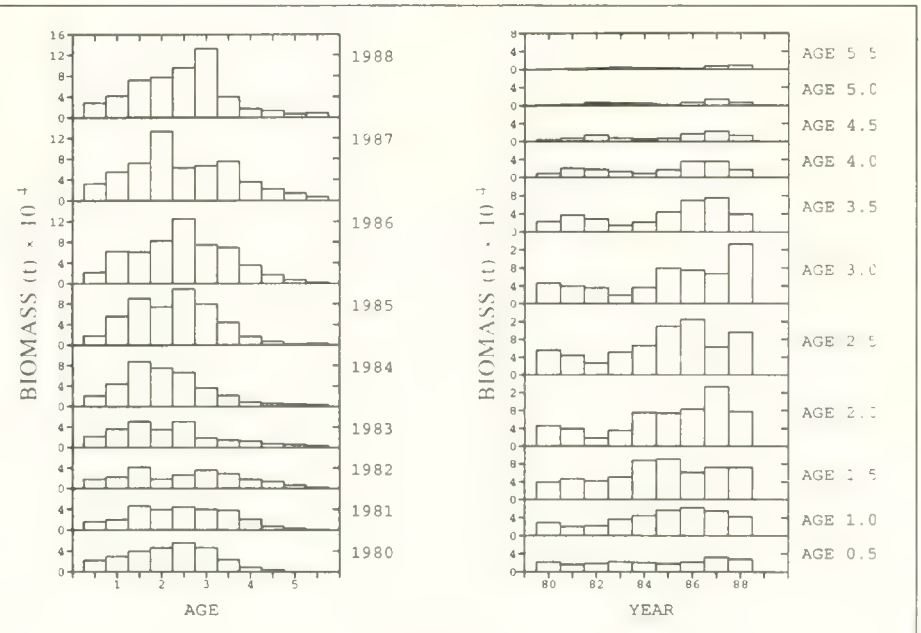

Figure 4

Estimated average annual biomasses (t) of yellowfin tuna (*Thunnus albacares*) by semi-annual age group for all effort directed at non-dolphin (Delphinidae) sets. In the left panel, biomasses are summarized by age within year. In the right panel, biomasses are summarized by year within age group. Age refers to the age in years at the middle of the year.

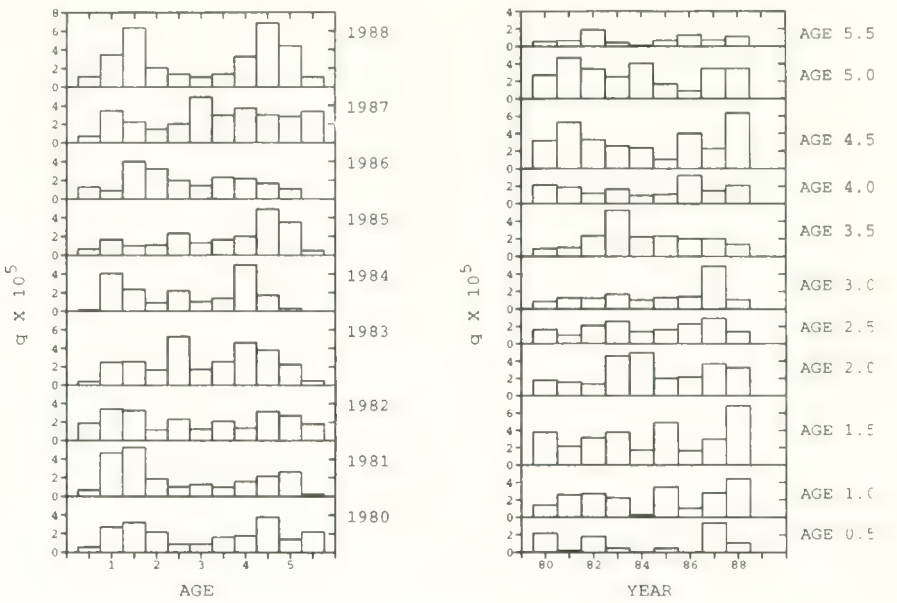

Figure 5

Average annual non-dolphin-set yellowfin tuna (*Thunnus albacares*) catchability coefficients (q in boat-days^{-1}) by semi-annual age group. In the left panel, coefficients are summarized by age within year. In the right panel, coefficients are summarized by year within age group. Annual catchability coefficients are estimated as the mean of the monthly coefficients. Age refers to the age in years at the middle of the year.

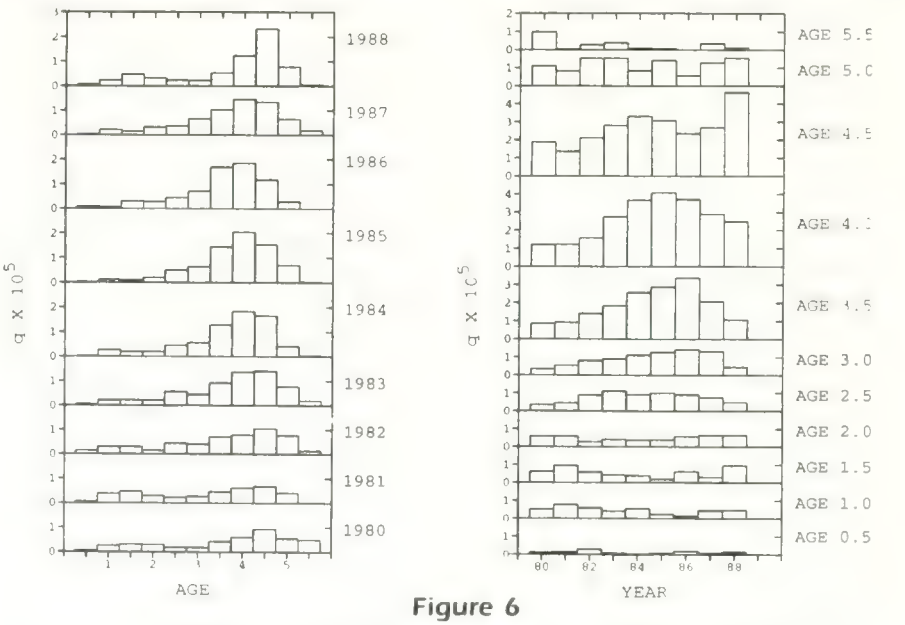

Figure 6

Average annual observed yellowfin tuna (*Thunnus albacares*) catchability coefficients (q in boat-days^{-1}) by semi-annual age group. In the left panel, coefficients are summarized by age within year. In the right panel, coefficients are summarized by year within age group. Annual catchability coefficients are estimated as the mean of the monthly coefficients. Age refers to the age in years at the middle of the year.

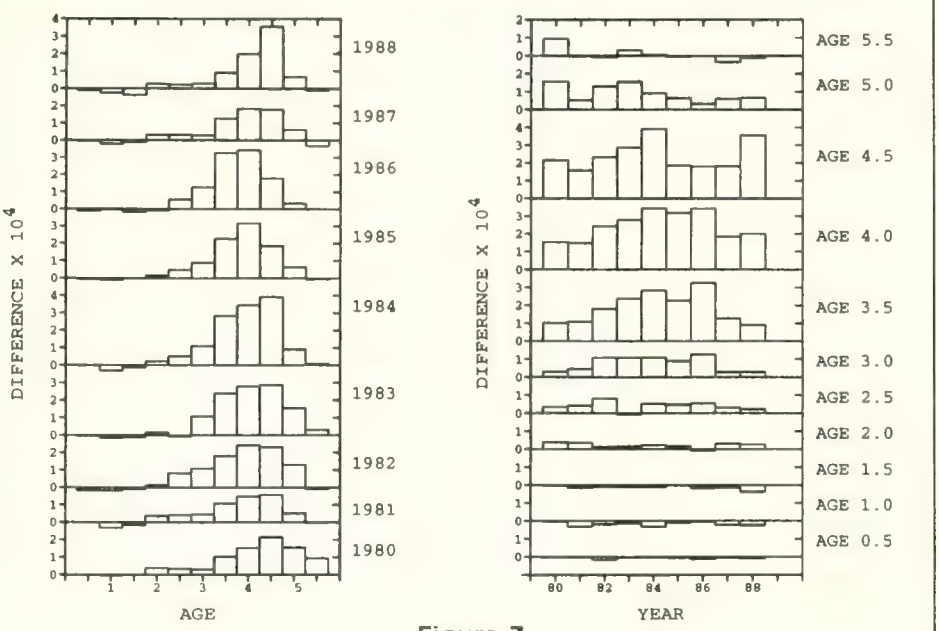

Figure 7

Average annual differences between the observed and non-dolphin (Delphinidae) catchability coefficients (boat-days^{-1}). In the left panel, differences are summarized by age within year. In the right panel, differences are summarized by year within age group. Age refers to the age in years at the middle of the year. Negative values (those pointing down) indicate that those non-dolphin-set catchability coefficients were greater than the observed coefficients.

the observed levels when the non-dolphin-set catchability coefficients were greater than or equal to the observed overall catchability coefficients (Fig. 7, negative values) for the age groups of the greatest biomass (Figs. 3 and 4). Estimated total yellowfin plus skipjack catches, if all effort were directed at non-dolphin sets, ranged from 84% during 1985 to 104% in 1983.

Estimates (Table 1, column QYF) of what the catches would have been without dolphin sets, using the quarterly average (over years) non-dolphin-set catchability coefficients for 1980–88, indicate that yellowfin catchabilities on non-dolphin sets increased in the late 1980's. Average quarterly catchability coefficients produced noticeably higher catches than the observed non-dolphin-set monthly coefficients in 1983–85 when the observed coefficients on small fish were low. On the other hand, average quarterly catchability coefficients produced lower catches during 1986–88, when the observed non-dolphin-set coefficients were high.

Monte Carlo simulation

The Monte Carlo simulations (Table 2) predicted that, if total effort, recruitment, and non-dolphin-set catchability coefficients had varied randomly throughout their 1980–88 distributions, and current levels of effort and recruitment had been maintained, changing to a fishery with all effort directed toward non-dolphin sets would have resulted in an average reduction of 55,563 t (24.7%) of yellowfin catch per year. The 95% confidence interval, based on the 50th and 950th highest simulated differences was 24,000 to 91,000 t (10%–42%). The entire frequency distribution of the differences between the two fishing-mode models in the 9th year is shown in Figure 8. Simulated recruitment estimates were selected from the observed values during 1980–88. Thus, average recruitment used in the simulations was higher than the mean actual recruitment to the initial 1980 population structure, which was partly a result of the poor recruitment during 1978 and 1979. Consequently, simulated catches were higher for both the observed mixed mode fishery (229,000 t per year) and the non-dolphin-set only fishery (175,000 t).

Yield per recruit

Estimated yellowfin catches from both the deterministic approach (Table 1) and the Monte Carlo simu-

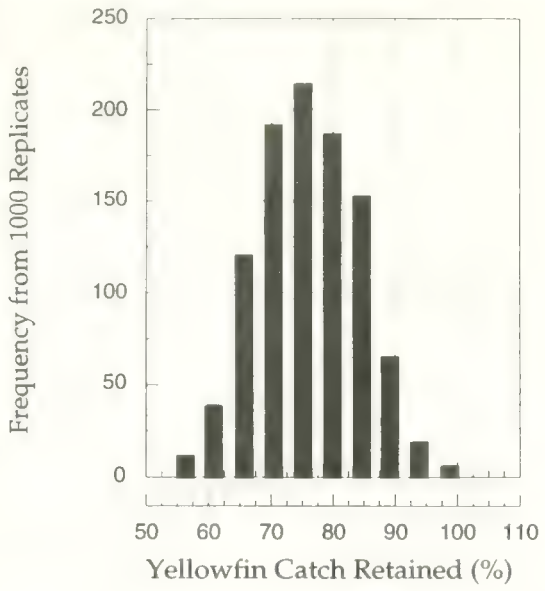

Figure 8

Frequency distribution of the percent of the yellowfin tuna (*Thunnus albacares*) catch in weight retained in the ninth year of a ban on dolphin (Delphinidae) sets, from 1,000 Monte Carlo simulated replicates. The percent of catch retained is calculated as 100× (the catch if all effort were directed at non-dolphin sets) / (the catch from the observed mixture of set types).

lations (Table 2) were heavily influenced by the recruitment and fishing effort levels used. Recruitment in the future may be different from that of past, because of changes in population size, age structure, and environmental factors. Therefore, actual future catches could be different from what we estimated. For these reasons, results in terms of reduction in yield per recruit are of interest. We estimated that the change to non-dolphin sets only would result in the reduction of the yield per recruit of yellowfin from the observed value of 2.8 kg per recruit to 2.1 kg as shown in Figure 9. In addition, effort levels could change in the future, perhaps as a reaction to the moratorium. Therefore, estimates of yield per recruit for various levels of effort might be useful. If effort levels change in the future, the multipliers on the *X*-axis in Fig. 9 could be used to estimate the potential yellowfin catch.

Discussion

In order to predict what the tuna catches might be in the future if there were a moratorium on dolphin sets, we estimated what the tuna catches would have been during 1980–88, had there been a moratorium on dolphin sets beginning in 1980. Using these estimates to predict future catches required the following assumptions:

1 Age-specific, non-dolphin catchability coefficients will be the same in the future as during 1980–88.
2 Fishing effort will remain at 1980–88 levels.
3 The geographic distribution of effort will be the same as during 1980–1988 (Fig. 2, A and B combined).
4 Recruitment will be at 1980–88 levels.
5 Natural mortality will not change in the future.
6 Skipjack abundance will not significantly change.

Significant deviations from these assumptions could make our estimates less valid. Therefore, the potential ramifications of deviations from the assumptions are discussed in detail below.

Major changes in the vulnerability of non-dolphin-associ-

Table 2

Monte-Carlo simulated annual yellowfin tuna (*Thunnus albacares*) catches, in thousands of tons, from 1980–88, quarterly, average catchability coefficients.

YEAR	OYFM	OYFL	OYFU	NYFM	NYFL	NYFU	PCM	PCL	PCU
1	202	184	229	150	121	186	72	61	83
2	215	183	247	164	127	205	76	62	89
3	227	183	276	170	129	217	76	59	91
4	229	183	283	175	131	223	70	68	88
5	236	188	286	181	139	230	76	59	91
6	245	195	302	187	138	241	76	61	91
7	237	189	294	180	138	229	75	59	90
8	231	182	281	176	134	228	76	58	91
9	229	181	279	174	131	222	75	58	90

OYFM = mean yellowfin tuna catch for the observed mixture of set types.
OYFL = OYFM lower 95% confidence interval.
OYFU = OYFM upper 95% confidence interval
NYFM = mean yellowfin tuna catch using total effort and non-dolphin catchability coefficients.
NYFL = NYFM lower 95% confidence interval
NYFU = NYFM upper 95% confidence interval
PCM = mean percent of catch retained (100 x NYFM/OYFM)
PCL = PCM lower 95% confidence interval.
PCU = PCM upper 95% confidence interval.

ated yellowfin to purse seiners could result in significantly different catches than we estimated. Allen and Punsly (1984) showed that both environmental and vessel efficiency factors affect the catchability of yellowfin by purse seiners in the EPO. Improvements in vessel efficiency could increase future catchability coefficients; whereas, environmental factors could produce either higher or lower catchability coefficients than those observed during 1980–88. Environmental factors affecting catchability could conceivably mask the effects of a moratorium on dolphin sets for several years. For example, if a moratorium on dolphin sets had been imposed at the beginning of 1983, the low catch in 1983 would have made it appear that the decline resulted from the moratorium. However, we predicted that a moratorium would have had the smallest effect in 1983 (Table 1). Fishermen, biologists, and managers should be aware that catches during the first year after a moratorium starts may not be indicative of long-term averages. However, since 9 years of data were used, our long-term average estimates should only be affected by long-term changes in catchability.

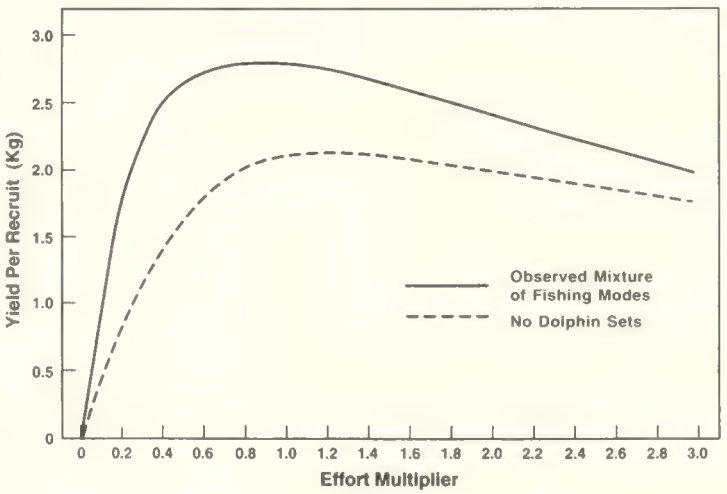

Figure 9

Yield per recruit of yellowfin tuna (*Thunnus albacares*) (kg) for the observed 1980–88 fishery (solid line) and a fishery with all effort directed at non-dolphin (Delphinidae) sets (dashed line). An effort multiplier of 1.0 refers to the 1980–88 average effort.

An assumption that effort will be lower in the future may be more realistic than our assumption that effort will remain at 1980–88 levels. However, we could not predict the extent to which effort might be reduced because it is affected by ex-vessel tuna prices at canneries all over the world, the prices of other foods, and the cost of fuel. Nevertheless, if we could estimate what the effort reductions would be in the future, the effort multipliers in the the yield-per-recruit estimates in Fig. 9 could still be used.

If the fishery contracted into the traditional inshore school- and log-set areas after a moratorium on dolphin sets, then catches may be lower than we estimated them to be. For example, if the area fished were smaller, and mixing between the fish inside and outside the area were incomplete, then the new fishing area would encompass fewer fish than the total area. Therefore, all of the population sizes of yellowfin used in the equations in the methods section would be overestimated. Recruitment estimates, which are estimates of the number of 30-cm yellowfin, would also be overestimated. In addition, if fishing effort remained high, but the range contracted, then a gear- competition effect might lower the catch of both yellowfin and skipjack. However, since effort levels are expected to decline after a moratorium, localized depletion of tuna due to a contracted fishery is unlikely.

We assumed that yellowfin recruitment in the future would not be affected by the changes in population size and age structure which might result from re-directing effort toward smaller fish, because a relationship between yellowfin spawning biomass and recruitment has not yet been demonstrated. However, a spawner-recruit relationship for yellowfin may be discovered in the future, because better estimates of yellowfin fecundity by size of fish, season, and area are currently being developed at IATTC. When this work is completed we may be able to predict recruitment levels and their resulting catches more accurately in the future. If future recruitment levels could be estimated, the future catches could be derived by multiplying the recruitment estimates by the yield per recruit shown in Figure 9.

Environmental factors have long been suspected of having significant effects on yellowfin recruitment. For example, favorable conditions in the late 1980's may have contributed to the large number of recruits (Bayliff, 1992). In 1987, the number of recruits was so large that the effect of a moratorium in 1988 would have been masked by a high catch of 1.5 year old yellowfin, first recruited during 1987. In 1988, the high abundance of 1.5 year old fish (Fig. 4) coupled with their high catchability for non-dolphin sets (Fig. 5) caused the estimated yellowfin catch if all effort were directed at non-dolphin sets to be almost as high as the estimated actual catch.

In order to predict future recruitment, the IATTC is currently studying the relationship between the environment and yellowfin recruitment. If they are successful the yield-per-recruit estimates in Figure 9 could be multiplied by the recruitment estimates to better predict future yellowfin catches.

Little is known about the rate of natural mortality of yellowfin. However, there is no reason to believe this rate will change. But, if it does change, a reasonable assumption would be that if natural mortality goes up, catch will go down and vice versa.

Little is known about skipjack population dynamics. We assumed that local depletion is negligible for skipjack. However, since skipjack are primarily caught in association with floating objects, if the amount of effort per floating object increases as a result of effort being re-directed from dolphin-associated tunas to floating objects, then the chances of depletion is certainly possible. If this occurs, our estimates of skipjack catch rates will be too high. This effect could be compounded during years in which floating objects are scarce, because the number of sets per floating object would increase. Since the skipjack catches have been increasing in the western Pacific Ocean, their abundance and catch in the eastern Pacific could be lower than our estimates.

A moratorium on dolphin sets is likely to result in reduced catchability, yield per recruit, average age, and total biomass of yellowfin. The catch of yellowfin, based on these factors only, was predicted to decline by approximately 55,600 t (25%). On the other hand, skipjack catches could increase, making the reduction in total tuna catches much smaller (4%). The effects of reductions in fishing effort, the range of the fishery, and recruitment were not analyzed in this study because they are currently unpredictable; however, all three would result in an additional decrease in total tuna catches. If better predictions of effort levels and yellowfin recruitment are made, the yield-per-recruit estimates in Figure 9 could be used in conjunction with them to better predict yellowfin catches. The results of our analysis indicate that catches in the first years after a moratorium begins may not be indicative of the long-term catches. Fishermen, biologists, and managers should not consider these first-year catches as indices of future catches, because recruitment and catchability vary annually. On the other hand, our estimates of future average catches should be useful unless there are long-term changes in catchability or recruitment.

Acknowledgments

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Literature cited

Abramson, N. J.
1971. Computer programs for fish stock assessment. F.A.O. Fish. Tech. Pap. 101, 154 p.

Allen, R. L.
1981. Dolphins and the purse-seine fishery for yellowfin tuna. I.A.T.T.C. Int. Rep. 16, 23 p.

Allen, R. L., and R. G. Punsly.
1984. Catch rates as indices of abundance of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean. I.A.T.T.C. Bull. 18(4):301–379.

Bartoo, N. W., and A. L. Coan.
1978. Changes in yield per recruit of yellowfin tuna (*Thunnus albacares*) under the ICCAT minimum size regulation. I.C.C.A.T. Col. Vol. Sci. Pap. 8(1):120–183.

Bayliff, W. H. (ed.)
1990. Annual report of the Inter-American Tropical Tuna Commission 1989, 288 p.
1992. Annual report of the Inter-American Tropical Tuna Commission 1991, 271 p.

Calkins, T. P.
1965. Variation in size of yellowfin tuna within individual purse-seine sets. I.A.T.T.C. Bull. 10(8):463–524.

Cole, J. S.
1980. Synopsis of biological data on the yellowfin tuna, *Thunnus albacares* (Bonnaterre, 1788), in the Pacific Ocean. I.A.T.T.C. Special Rep. 2:71–150.

Green, R. E.
1967. Relationship of the thermocline to success of purse seining for tuna. Am. Fish. Soc., Trans. 96(2):126–130.

Greenblatt, P. R.
1979. Association of tuna with flotsam in the eastern tropical Pacific. Fish. Bull. 77(1):147–155.

Gulland, J. A.
1965. Estimation of mortality rates. Annex to Rep. Arctic Fish. Working Group, Int. Counc. Explor. Sea C.M. 1965(3), 9 p.

Hennemuth, R. C.
1957. Analysis of methods of sampling to determine the size composition of commercial landings of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*). I.A.T.T.C. Bull. 2(5):174–243.

Holt, S. J.
1958. A note on the simple assessment of a proposal for mesh regultaion. I.C.N.A.F. Annual Proc. 8(4):82–83.

Jones, R.
1961. The assesment of the long term effects of changes in gear selectivity and fishing effort. Mar. Res. Scot. 1961(2), 19 p.

Joseph, J., and T. P. Calkins.
1969. Population dynamics of the skipjack tuna (*Katsuwonis pelamis*) of the eastern Pacific Ocean. I.A.T.T.C. Bull. 13(1), 273 p.

Orange, C. J., and T. P. Calkins.
1981. Geographical distribution of yellowfin and skipjack tuna catches in the eastern Pacific Ocean, and fleet and total catch statistics 1975–1978. I.A.T.T.C. Bull. 18(1):1–120.

Pope, J. G.
1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. Northwest Atl. Fish. Res., Bull. 9:65–74.

Punsly, R. G.
1983. Estimation of the number of purse-seiner sets on tuna associated with dolphins in the eastern Pacific Ocean during 1959-1980. I.A.T.T.C. Bull. 18(3):227–299.

1987. Estimation of the relative annual abundance of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean during 1970–1985. I.A.T.T.C. Bull. 19(3):263–306.

Punsly, R. G., and R. B. Deriso.
1991. Estimation of the abundance of yellowfin tuna, *Thunnus albacares*, by age groups and regions within the eastern Pacific Ocean. I.A.T.T.C. Bull. 20(2):98–131.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

Tomlinson, P. K., S. Tsuji, and T. P. Calkins.
1992. Length frequency estimation for yellowfin tuna. I.A.T.T.C. Bull. 20(6):357–398.

Wild, A.
1986. Growth of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean based on otolith increments. I.A.T.T.C. Bull. 18(6):423–482.

Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea

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Abstract.— Gastrointestinal tract contents were evaluated from 73 female and juvenile male northern fur seals (*Callorhinus ursinus*) for analysis of their diet in the Bering Sea. Fur seals were collected from August to October of 1981, 1982, and 1985. Juvenile walleye pollock (*Theragra chalcogramma*) and gonatid squid were the primary prey. Pacific herring (*Clupea pallasi*) and capelin (*Mallotus villosus*), considered important fur seal prey in previous reports, were absent from the diet. Prey species and size varied among years and between nearshore and pelagic sample locations. Interannual variation in the importance of pollock in the diet of fur seals was positively related to year-class strength of pollock. Midwater (n=23) and bottom (n=116) trawls were conducted at the location of fur seal collections to determine availability of fish and squid relative to prey species eaten by fur seals. The species and size composition of prey taken by fur seals was similar to midwater trawl collections, but differed from bottom trawl catches. Contrary to earlier conclusions that northern fur seals are opportunistic in their feeding habits, we conclude that fur seals are size-selective midwater feeders during the summer and fall in the eastern Bering Sea.

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The Pribilof Island population (St. George and St. Paul Islands) of northern fur seals (*Callorhinus ursinus*) represents approximately 75% of the total species breeding population. Between 1975 and 1981, the Pribilof Island population declined from 1.2 million to an estimated 800,000 animals (York and Hartley, 1981; Fowler, 1985). Abundance levels on St. Paul Island appear to have stabilized (York and Kozloff, 1987) at a level 60–70% below estimates of the 1940's and 1950's, and at one-half the estimated carrying capacity (Fowler and Siniff, 1992). The number of animals continues to decline on St. George Island (York, 1990).

The objectives of this study were to determine the species and size of prey eaten by northern fur seals in the eastern Bering Sea, to compare the seals' present diet with that prior to the population decline, and to examine the seals' consumption of prey relative to prey availability. Previous studies on the feeding habits of northern fur seals in the eastern Bering Sea (Scheffer, 1950a; Wilke and Kenyon, 1952; Wilke and Kenyon, 1957; North Pacific Fur Seal Commission Reports 1962,[1] 1975,[2] and 1980[3]; Fiscus et al., 1964; Fiscus et al., 1965; Fiscus and Kajimura, 1965) were conducted prior to the 1975–81 population decline and prior to the 1970's development of a commercial walleye pollock (*Theragra chalcogramma*) fishery in the Bering Sea. Neither the size of fur seal prey, nor fur seal selection of prey relative to real-time availability have been previously examined in detail.

Methods

Northern fur seals were collected from 17 to 28 October 1981; from 24 September through 6 October

[1] North Pacific Fur Seal Commission Report on Investigations from 1958 to 1961: Presented to the North Pacific Fur Seal Commission by the Standing Scientific Committee on 26 November 1962, 183 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.

[2] North Pacific Fur Seal Commission Report on Investigations from 1967 through 1972: Issued from the headquarters of the Commission, Washington, D.C., June 1975, 212 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.

[3] North Pacific Fur Seal Commission Report on Investigations during 1973–76: Issued from the headquarters of the Commission, Washington, D.C., February 1980, 197 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.

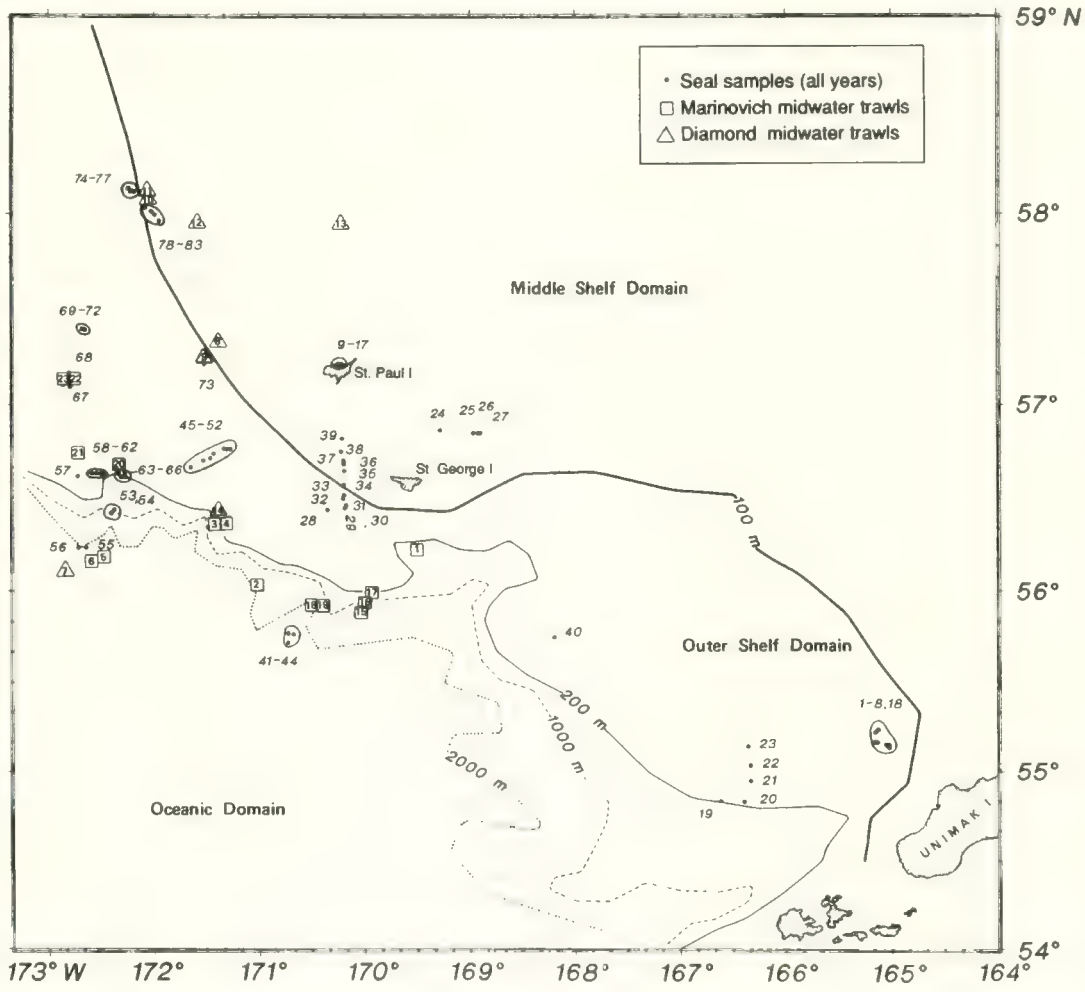

Figure 1

The study area with midwater trawl locations and northern fur seal collection positions. All midwater trawls were conducted in 1985. Seal numbers 1–17 were collected in 1981, 18–40 were collected in 1982, and 41–83 were collected in 1985.

1982; and from 6 to 16 August 1985. Collections were made within 185 km of the Pribilof Islands over the continental shelf, continental slope, and oceanic domain of the eastern Bering Sea (Fig. 1).

Seals were shot from a small craft and returned to the NOAA ship *Miller Freeman* (65–m stern trawler) for examination within 1.5 hours of collection. The esophagus of each seal was checked for food as an indication of regurgitation, and the gastrointestinal (GI) tract was removed and frozen. Gastrointestinal tract contents were later thawed and gently rinsed through a series of graded sieves (0.71, 1.00 or 1.40, and 4.75 mm in 1981 and 1982; 0.50, 1.00, 1.40, and 4.75 mm in 1985). Fleshy remains were preserved in 10% formalin. Fish otoliths and bones were stored dry. Cephalopod rostra and statoliths were preserved in 70% isopropyl alcohol.

Prey identification was based on all remains, including otoliths. Otoliths were not used for fish identification in earlier fur seal diet studies because stomach samples were stored in formalin, which dissolves otoliths. Techniques and references for the identification of prey based on otoliths include Fitch and Brownell (1968), Morrow (1979), Frost and Lowry (1981), and otolith reference collections (see Acknowledgments). References for cephalopod beak and statolith identification include Clarke (1962), Young (1972), Roper and Young (1975), Clarke (1986), and beak and statolith reference collections (see Acknowledgments). A tooth was collected from each fur seal that was shot and ages were derived from direct readings of canine tooth sections follow-

ing Scheffer (1950b). In the analysis of data, males and females of all ages were treated as one group because of small sample sizes.

The highest number of either upper or lower cephalopod beaks and left or right otoliths was recorded as the maximum number of each species present. If deterioration made some left and right otoliths of a species indistinguishable, they were counted and the total was divided by 2. The frequency of occurrence and number of individuals from each prey taxon was calculated for each seal.

The fork length (FL) of pollock and dorsal mantle length (DML) of squid was measured directly when whole prey were present in the stomachs. In the absence of whole prey, body size was estimated by measurement of otoliths and beaks. The maximum length of pollock otoliths and lower rostral length (LRL) of gonatid squid beaks were measured to the nearest 0.05 mm with vernier calipers. Squid DML's were estimated by comparison of LRL measurements to the LRL/DML relationship of 51 gonatid squid caught in trawls conducted in the vicinity of seal collections. Walleye pollock fork lengths were estimated by regression against otolith length (Frost and Lowry, 1981). For otoliths measuring:

$$>10.0\text{mm, (FL) } Y = 3.175X - 9.770 \; (R = 0.968)$$

$$\leq 10.0\text{mm, (FL) } Y = 2.246X - 0.510 \; (R = 0.981).$$

Walleye pollock ages were estimated from these lengths based on length-age relation described by Smith (1981) and Walline (1983) for walleye pollock from the Bering Sea.

Otoliths may dissolve or erode to varying degrees depending on their size and duration in fur seal stomachs. We evaluated the bias introduced in FL estimates due to eroded otoliths by assigning otoliths to four condition categories (excellent, good, fair, and poor) based on amount of wear. After quality categorization, the maximum lengths of otoliths (except those in "poor" condition) were measured for estimation of body length by regression, and length frequencies of each category were determined independently.

Cephalopod beaks are more resistant to digestion than otoliths and were typically identifiable. Beaks with chipped, worn, or broken rostra were rare and were not measured. Cephalopod beaks were identified to species when possible, but most were categorized into two groups referred to as *Gonatopsis borealis-Berryteuthis magister* or *Gonatus madokai-Gonatus middendorffi*. The two individual species within each group can be separated based on their external morphology and statolith structure, but cannot presently be separated based on beak structure alone (Clarke, 1986).

Trawl collections of potential seal prey

Trawls were conducted throughout the study area from the *Miller Freeman* between 1900 and 0600 hours within the vicinity of seal collections (Fig. 1). Both bottom and midwater trawls were conducted to provide a relative measure of the availability and size of potential fur seal prey species. Bottom trawls were made at 52–498 m ($\bar{x}$=139 m) depths with an 83/112 Eastern bottom trawl (17–m width, 2.3–m height mouth opening; 3.2–cm codend liner mesh; 360–mesh circumference; 200–mesh depth; 30–m bridle). Thirty-nine bottom trawls were conducted in 1981 (14 October–4 November), 51 in 1982 (24 September–8 October), and 26 in 1985 (5 August–22 August). Seven 1985 trawls were made beyond maximum recorded dive depths of adult female seals (257 m; Ponganis et al., 1992). They were included in analyses because the species and size of fish and squid caught were consistent with those caught by bottom trawl within seal dive depths.

Collection and sorting methods and calculation of bottom trawl catch per unit of effort (CPUE) values followed Smith and Bakkala (1982). The total bottom trawl catch was randomly split into a sample of about 2500 kg. Individual species of fishes were identified and weighed (wet) and CPUE (no./ha) was estimated based on distance trawled. In 1981 and 1982, cephalopods were classified as squid or octopus and discarded. In 1985, all cephalopods were identified, sexed, weighed, and frozen whole. Beaks were extracted and stored in 70% isopropyl alcohol.

Sex and age determination and body length measurements were made on a subsample of up to 200 walleye pollock from each trawl. Fork lengths were measured to the nearest centimeter. Saccular otoliths were collected for age determination (Smith and Bakkala, 1982) and stored in 70% isopropyl alcohol. Walleye pollock CPUE was calculated by age and body length. For purposes of this study, age-length frequencies for male and female walleye pollock were combined for each of the three years.

Midwater trawls were made in 1985 with a Diamond midwater net (n=8) (10–16 fm mouth opening; 3.2–cm codend liner mesh; 354–mesh circumference; and 160–mesh depth with 2–m bridles) and a Marinovich herring trawl (n=15) (6.1–m width, 6.1–m height mouth opening; 1–cm codend liner mesh; 150–mesh circumference; and 350–mesh depth with 10–m bridles). Specific trawling positions were chosen within the vicinity of northern fur seal collection areas based on the presence of fish or squid as

indicated on 38 kHz echosounders and a chromoscope. Midwater towing depths measured by an attached transducer ranged from 22 to 340 m (x=143 m).

All species of fish and cephalopods collected in midwater trawls were identified and counted. The CPUE and frequency of occurrence of each species, LRL and sex of gonatid squid, and walleye pollock frequency of occurrence by age and length were calculated separately for each trawl type.

Comparison of seal diet and trawl collections

The Odds Ratio (Fleiss, 1981) was used to compare prey availability (as determined by midwater and bottom trawls) with selection of prey by fur seals for each sample year:

$$O = \frac{p^1 q^2}{p^2 q^1},$$

where p1 = % of diet comprised by a given prey taxon,
q1 = % of diet comprised by all other prey taxon,
p2 = % of food complex in environment comprised by a taxa, and
q2 = % of food complex in environment comprised by all other taxa.

Values were calculated for number of each prey species and percent frequency of occurrence among seals, and CPUE values (no./ha) for each trawl type. Values for $p2$ and $q2$ were also calculated for the trawl types combined in order to provide a comprehensive description of the water column. The natural log of the calculated Odds Ratio represents either positive or negative selection. The Odds Ratio was chosen because, unlike other electivity indices, the significance of the distance of calculated values from zero (null hypothesis that prey were consumed non-selectively) can be tested with the Z-statistic (Gabriel, 1978).

In order to quantify the degree of overlap in the composition of bottom trawls, midwater trawls and fur seal GI contents, percent similarity (PS) values (Langton, 1982) were calculated:

$$PS = 100 - 0.5 \sum a - b,$$

where a = % number of a given prey for seals, and
b = % number of the same prey for trawls.

Results

Fur seal diet

Eighty-three fur seals were collected. Ten of the 17 GI tracts collected in 1981 were empty and were excluded from the analysis. Of the 73 animals included in the analysis, 13 were juvenile males, 3 were juvenile females and 57 were adult females. Most fur seals were collected over depths less than 200 m within the outer shelf domain (Fig. 1).

Fish represented 89% and cephalopods 11% of prey numbers for all three sample years combined. One-hundred percent of the GI tracts had fish remains and 82% of all samples contained walleye pollock. A total of 2,658 walleye pollock otoliths were measured. In all years combined, juvenile walleye pollock (3–20 cm FL) were the most numerous and frequently occurring prey species. Sixty-five percent of prey walleye pollock were from the 0–age group (3–13 cm FL) and 31% were from age group 1 (13–20 cm FL). Only 4% of prey pollock were from age group 2 (20$^+$ cm FL) and older.

Gonatid squids occurred in 36% of the samples, but in comparison with pollock, they were not consumed in large numbers (Fig. 2). *Gonatus madokai-G. middendorffi* and *Gonatopsis borealis-Berryteuthis magister* were the second most frequently occurring prey in all years combined. Seventy-nine percent of the 389 beaks measured were from squid 5–12 cm DML.

Northern smoothtongue (*Leuroglossus schmidti*), a bathylagid deepsea smelt, was the second most numerous fish prey overall (Fig. 2) even though it was found only in 1985 (Table 1). Northern smoothtongue composed a higher percentage of the total number of fish than walleye pollock ≥2 years old for all sample years combined. Atka mackerel (*Pleurogrammus monopterygius*) composed 23.9% of the 1981 prey sample and was present in five of seven stomachs collected in 1981 that had prey remains, but the species was identified from the prey remains of only one other individual among the six collected in the same area in 1982 (Table 1).

Although walleye pollock were eaten by fur seals in all 3 years, marked differences in age and body size were found between years (Table 1; Fig. 3). In 1981, the few walleye pollock otoliths found were from fish 3–4 years of age. Fur seal GI tracts contained primarily age-0 pollock in 1982 and age-1 pollock in 1985. Exclusion of otoliths that were in fair condition caused a downward shift in modal FL frequencies of 1 to 2 cm, but did not change our estimation of the age categories of pollock eaten by fur seals.

The species of forage fishes and squids consumed by fur seals varied between samples taken on and off the continental shelf (200 m) (Fig. 4). The GI tracts of fur seals collected over oceanic and continental slope regions contained primarily northern smoothtongue and squids, especially *Gonatopsis*

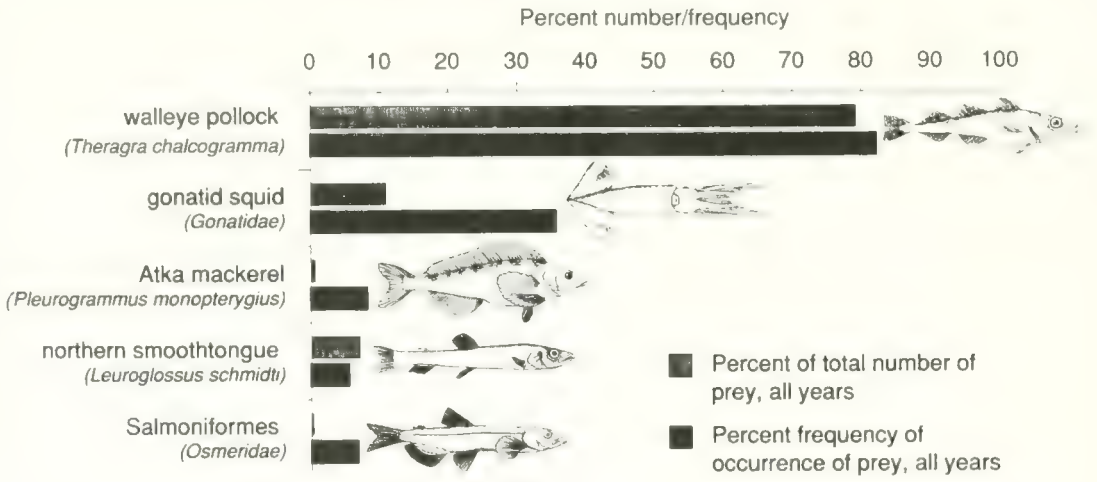

Figure 2

Percent of total number and frequency of occurrence of primary prey in northern fur seal (*Callorhinus ursinus*) gastrointestinal tracts for sample years 1981, 1982, and 1985 combined. Species shown include the top three prey from each sample year.

borealis-Berryteuthis magister. Seals collected over the continental shelf contained the remains of walleye pollock of all ages and squids, especially *Gonatus madokai-G. middendorffi*. Adult walleye pollock, although rare in stomach contents, were found in greatest frequency in fur seals collected from the outer domain of the continental shelf. Juvenile walleye pollock were consumed primarily over the midshelf and outer domain. Atka mackerel was found only in samples collected over the outer shelf domain north of Unimak Island.

Comparisons with trawl samples

Of the five top-ranked species collected in bottom trawls, only walleye pollock was found in fur seal GI contents (Figs. 2 and 5). Walleye pollock from bottom trawls ranged from 1 to over 12 years of age and had mean body lengths of 38.9 cm (3–4 years old) in 1981, 39.7 cm (4–5 years old) in 1982, and 44 cm (5–6 years old) in 1985 (Fig. 6). All but four of the cephalopods caught in 1985 bottom trawls were *Berryteuthis magister* ranging from 17.5 to 31.2 cm DML ($\bar{x}$=21.6). As in the seal samples, *B. magister* was collected in trawls conducted over the outer continental shelf domain along the 200–m contour, or over the continental slope between 200 and 1000 m. Otherwise, the bottom trawl catch for all three years was so dissimilar to the midwater trawl catch (Figs. 5 and 6) and fur seal GI contents (Fig. 2) that electivity computations were not meaningful (Odds Ratio=0).

Calculation of the Odds Ratio and *Z*-statistic on 1985 data with midwater and bottom trawl catch combined showed statistically significant positive selection by fur seals for age-0 pollock (P=0.0002), age-1 pollock (P<0.0001), northern smoothtongue (P<0.0001), and gonatid squid (P=0.02). Negative selection for adult walleye pollock was suggested but was not statistically significant (P=0.13).

A similarity index of 81% was calculated for species composition and prey size in the 1985 GI samples and midwater trawls. Fur seals fed on three of the four top-ranked species caught in midwater trawls (Figs. 2 and 5). Midwater trawls and seals caught predominantly juvenile walleye pollock. Gonatid squids (*Gonatus madokai*, *G. middendorffi*, and *Gonatopsis borealis*) had low CPUE values but were second in frequency of occurrence in both fur seal GI tracts and midwater trawls. The modal length of walleye pollock and gonatid squids was 5–20 cm in both midwater trawl and GI samples in 1985. Few adult walleye pollock and no large squid were collected in midwater trawls or seal GI samples.

Seals and midwater trawls caught the same prey species at the same general locations on and off the continental shelf (Fig. 4). As in GI contents, age-0 and age-1 walleye pollock were collected in midwater trawls made on the middle and outer shelf and near the continental slope. *Gonatopsis borealis* were found on the continental slope and near-slope. *Gonatus madokai* and *G. middendorffi* were found throughout the sampling area, but primarily on the outer continental shelf and near-slope sampling areas.

Table 1

Gastrointestinal contents of 73 northern fur seals (*Callorhinus ursinus*) collected from the Bering Sea in 1981 (n=7), 1982 (n=23), and 1985 (n=43). Tentative identifications are designated as (t).

	% number in each year			% frequency occurrence		
Prey species	1981	1982	1985	1981	1982	1985
Fish						
Clupea pallasi	—	0.1	—	—	4.4	—
Osmeridae (t)	8.7	—	—	42.9	—	—
Salmonidae	5.4	—	—	42.9	—	—
Leuroglossus schmidti	—	—	12.7	—	—	9.3
Gadus macrocephalus (t)	—	—	0.1	—	—	7.0
Theragra chalcogramma	54.4	87.3	74.1	100	95.7	72.1
3–5cm fork length	—	(8.8)	(5.7)			
5–10cm fork length	(4.3)	(63.9)	(2.3)			
10–20cm fork length	—	—	(55.6)			
>20cm fork length	(38.0)	(1.4)	(1.7)			
T. chalcogramma (t)	—	0.1	0.1	—	8.7	4.7
unidentified Gadidae	—	—	0.9	—	—	20.9
Lycodes sp.	1.1	—	0.5	14.3	—	—
Pleurogrammus monopterygius	23.9	0.1	—	71.4	4.4	—
P. monopterygius (t)	—	0.1	—	—	4.4	—
unidentified percoid	1.1	—	—	14.3	—	—
unidentified fish	5.4	0.4	0.5	14.3	13.0	25.6
Squid						
Gonatus berryi	—	—	0.1	—	—	2.3
G. pyros	—	—	0.1	—	—	2.3
G. tinro	—	—	0.1	—	—	2.3
G. tinro (t)	—	—	0.1	—	—	2.3
Gonatus madokai-middendorffi	—	0.1	4.8	—	4.4	34.9
Gonatus sp.	—	—	0.1	—	—	2.3
Berryteuthis magister	—	0.6	—	—	8.7	—
Gonatopsis borealis-B. magister	—	10.2	6.4	—	17.4	20.9
unidentified Gonatidae	—	—	0.1	—	—	7.0
unidentified squid	—	1.0	—	—	34.8	—
Total number prey	92	1638	2189			
Total number fish	92	1445	1936	100	100	100
Total number squid	0	193	253	0	52.2	46.5

Discussion

The modal size distribution of walleye pollock in GI contents of female and juvenile male fur seals reflected year-class strength projections of walleye pollock (Fig. 7). Walleye pollock have highly variable recruitment rates (Smith, 1981), and year-class strength varied five-fold between 1977 and 1982 (Bakkala et al., 1987). Population estimates based on bottom trawl and midwater acoustic surveys in the eastern Bering Sea indicated that the 1980 year class (age 1 in 1981) was about half the average year-class size; the 1981 year class (age 0 in 1981) was the weakest observed prior to 1983; and the 1978 year class (age 3 in 1981) was the strongest observed. The 1982 and 1984 year classes were strong and the 1985 year class was considered average (Bakkala et al., 1987). Similarly, walleye pollock as prey in 1981 were primarily adults 3 and 4 years of age (from the 1977 and 1978 year class); in 1982, seals ate age-0 pollock exclusively; and in 1985, prey pollock were primarily from the 1984 year class. The concordance of pollock recruitment and fur seal GI content analysis indicates that the variable recruitment of walleye pollock affects prey consumption by northern fur seals.

The three basic dive patterns described for adult females in the Bering Sea are shallow, pelagic nighttime diving (most commonly to 50–60 m); deep day-and-night diving over the continental shelf (most commonly to 175 m); and some combination of both, including shallow diving over the continental shelf

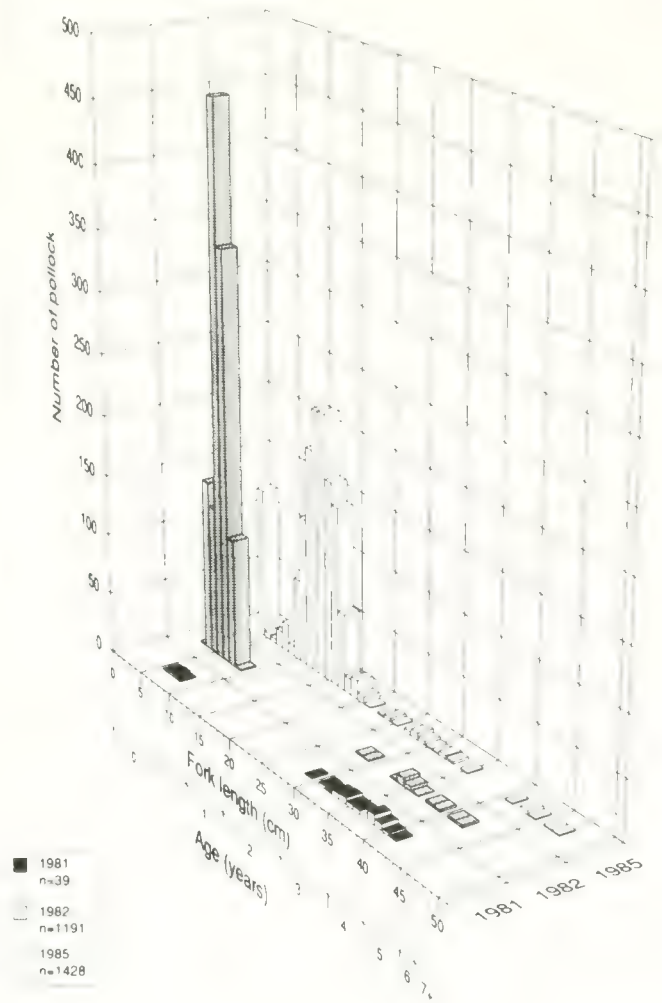

Figure 3

Age-length frequencies of walleye pollock (*Theragra chalcogramma*) based on otoliths in northern fur seal (*Callorhinus ursinus*) gastrointestinal tracts by year.

and both shallow and deep diving along the continental slope. Dive pattern information is based on time-depth recordings (Gentry et al., 1986; Loughlin et al., 1987; Goebel et al., 1991), radio telemetry (Loughlin et al., 1987), stomach volume estimates (Mead, 1953; Taylor et al., 1955[4]; Spalding, 1964; Wada, 1971; Kajimura, 1984), and stomach clearance studies (Miller, 1978[5]; Bigg, 1981[6]; Bigg and Fawcett, 1985; Murie and Lavigne, 1985).

Based on fur seal and trawl collections in this study and on distributional information of prey (Smith, 1981; Dunn, 1983; Kubodera and Jefferts, 1984; Lynde, 1984), shallow diving fur seals over the continental shelf concentrated on juvenile walleye pollock and juvenile gonatid squid (*Gonatus madokai-G. middendorffi*), while shallow divers off-shelf targeted juvenile gonatid squid (*Berryteuthis magister-Gonatopsis borealis*) and bathylagid smelt. Daytime deep diving over the continental shelf would be advantageous to seals concentrating on prey (i.e., adult walleye pollock) that tend to school at depth during daytime hours and disperse as they rise in the water column at night. Adult gonatid squid probably occur in schools at the bottom on the continental shelf and remain deep along the shelf edge during both day and night. The location and degree of concentration of prey may be closely associated with the hydrography of the foraging region. The hydrography of the foraging region may have the most direct influence on the diving patterns of fur seals.

Hydrographic characteristics of the Bering Sea continental shelf, include a two-layered midshelf and a three-layered outer shelf domain that may stratify and concentrate prey by species and age in a vertical plane. Nishiyama et al. (1986) proposed that vertical stratification within the eastern Bering Sea shelf serves as a "nursery layer" to confine young-of-the-year pollock in the upper 40 m of the water column within the boundary region between the upper and lower layers. Copepod nauplii are also concentrated in this area, providing a ready source of food for larval walleye pollock (Bailey et al., 1986). Wada (1971) determined that primary foods of fur seals off the Sanriku Coast in Japan consisted of migrating species closely related to boundary regions, especially transition zone regions. The horizontal temperature and salinity structures that occur on either side of frontal regions within our study area (Kinder and Schumacher, 1981) may

[4] Taylor, F. H. C., M. Fujimaga, and F. Wilke. 1955. Distribution and food habits of the fur seals of the North Pacific Ocean. Rept. of Coop. Invest. by the Govts. of Can., Japan, and the U.S.A. Feb.-July, 86 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.

[5] Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. Final Rep. to U.S. Mar. Mamm. Comm. MMC-75/08, 27p.

[6] Bigg, M. A. 1981. Digestion rates of herring (*Clupea harengus pallasi*) and squid (*Loligo opalescens*) in northern fur seals. Submitted to the 24th Annual Meeting of the Standing Sci. Comm., N. Pac. Fur Seal Comm., 6–10 April, Tokyo, Japan, Available: Alaska Fish. Sci. Cent., 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.

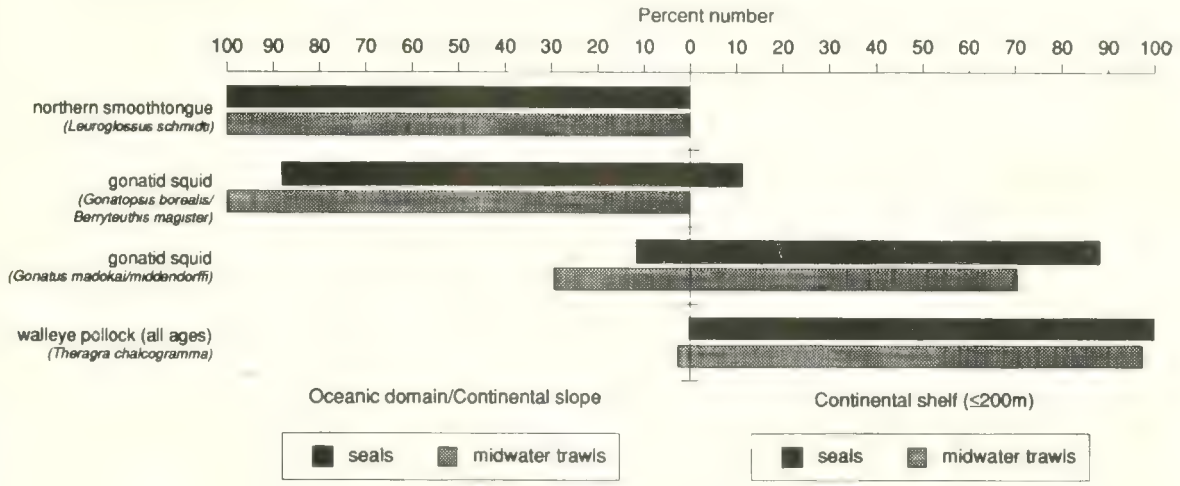

Figure 4

Primary species identified in fur seal (*Callorhinus ursinus*) gastrointestinal tracts and midwater trawls collected on and off the eastern Bering Sea continental shelf in 1985.

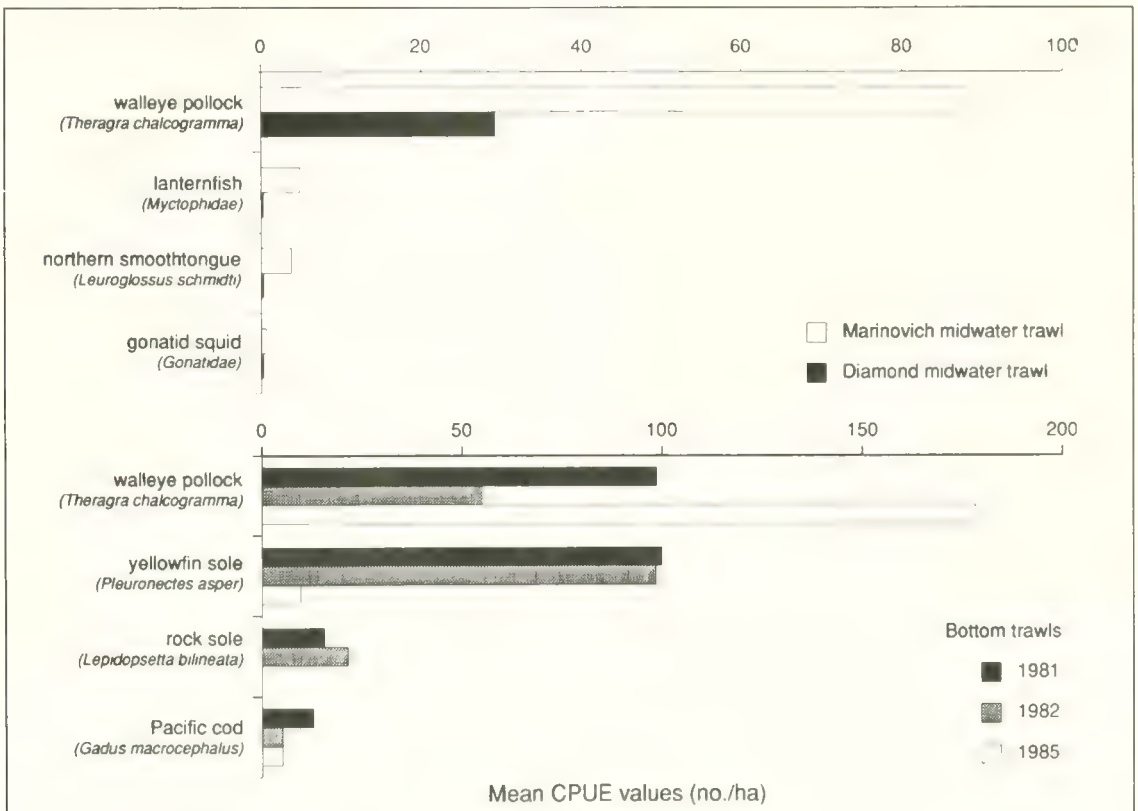

Figure 5

Catch per unit of effort (CPUE) number/hectare (no./ha) values for species caught in 1985 midwater trawls and bottom trawls in 1981, 1982, and 1985.

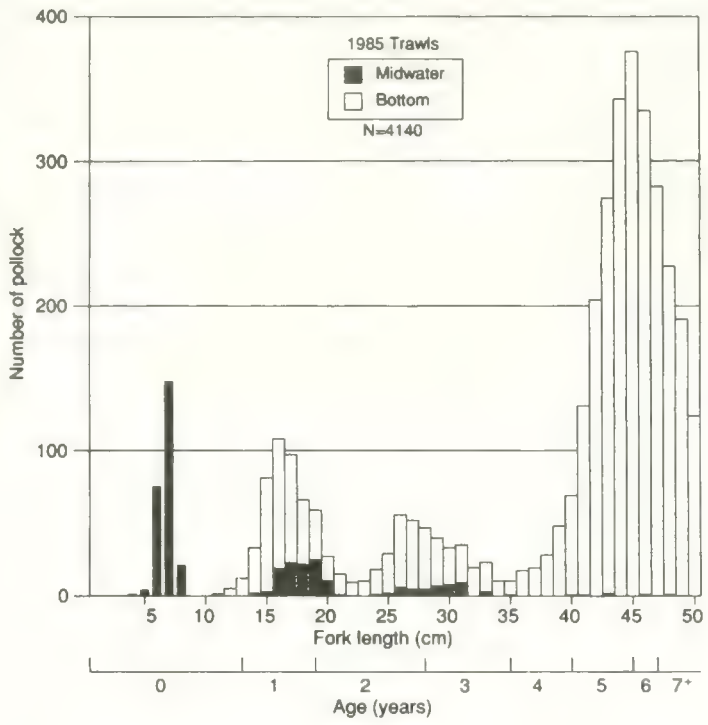

Figure 6

Age-length frequencies of walleye pollock (*Theragra chalcogramma*) collected in bottom and midwater trawls in 1985.

also form boundaries that concentrate prey. Diving depths of 175 m coincide with the depth break of the outer continental shelf. Diving depths of 50–60 m coincide with the depth break of the frontal systems between the midshelf and inner shelf.

Previous analyses of fur seal diet in the eastern Bering Sea were based primarily on a sample of 3,530 stomachs collected pelagically in 1960, 1962–64, 1968, 1973, and 1974 (North Pacific Fur Seal Commission Reports 1962,[1] 1975,[2] and 1980[3]; Fiscus et al. 1964; Fiscus et al. 1965; Fiscus and Kajimura 1965). Reviews of the pelagic data cite walleye pollock (Kajimura, 1985; Perez and Bigg, 1986), Pacific herring (*Clupea pallasi*), capelin (*Mallotus villosus*), Atka mackerel, gonatid squids (*Gonatus* spp., *Berryteuthis magister* and *Gonatopsis borealis*), and intermittently, northern smoothtongue (Kajimura, 1984) as principal fur seal prey in the eastern Bering Sea. Published reports and reviews of fur seal feeding habits prior to the pelagic collections (1892–1950's) also described walleye pollock, capelin, gonatid squid, and bathylagid smelt as primary prey in seal spewings or stomachs (Scheffer, 1950a; Wilke and Kenyon, 1952; Wilke and Kenyon, 1957).

In terms of prey species composition, the summer diet of female and juvenile male northern fur seals does not appear to have changed dramatically since the turn of the century. Pollock and gonatid squid are still the predominant prey of northern fur seals in the eastern Bering Sea. More subtle changes, such as a decrease in pollock size may have occurred (Smith, 1981; Swartzman and Haar, 1983) and could play a critical role in foraging success of northern fur seals. Unfortunately, records of prey size in historical fur seal diet studies are incomplete.

It should be noted that Pacific herring and capelin were absent from fur seal diets in this study, despite collections in areas where they occurred as important prey in the past. Fluctuation in the population status of Pacific herring and capelin in the Bering Sea has been attributed to the sporadic and localized nature of their abundance (Turner, 1886; Meek, 1916; Favorite et al. 1977[7]; Lowe 1991[8]), overharvesting and displacement by walleye pollock (Wespestad and Barton, 1981; Swartzman and Haar, 1983; Wespestad and Fried, 1983; Bakkala et al., 1987), and/or environmental change such as the pronounced warming in the Gulf of Alaska and Bering Sea over the past decade (Royer, 1989). The absence of these previously important prey may be critical to seals during successive years of weak walleye pollock year-class abundance.

Fur seals select juvenile walleye pollock as prey despite a wide availability of other prey types within their dive range. Fur seals may select their prey by size and schooling behavior, whether the prey are myctophids in oceanic waters off Japan (Wada, 1971); Pacific herring, capelin, market squid (*Loligo opalescens*) and Pacific whiting (=Pacific hake, *Merluccius productus*) in the eastern North Pacific (Kajimura, 1984; Perez and Bigg, 1986); or walleye pollock in the eastern Bering Sea (Kajimura, 1984). The most consistent prey characteristic between feeding studies across the northern fur seal range

[7] Favorite, F., T. Laevastu, and R. R. Straty. 1977. Oceanography of the northeastern Pacific Ocean and eastern Bering Sea, and relations to various living marine resources. NWAFC Proc. Rep. 280p. Alaska Fish. Sci. Cent., NMFS, NOAA, 7600 Sand Point Way NE., Bin C15700, Seattle, WA 98115–0070, 280p.

[8] Lowe, S. A. 1991. Atka mackerel. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1992, p. 11–2 to 11–40. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, AK 99510.

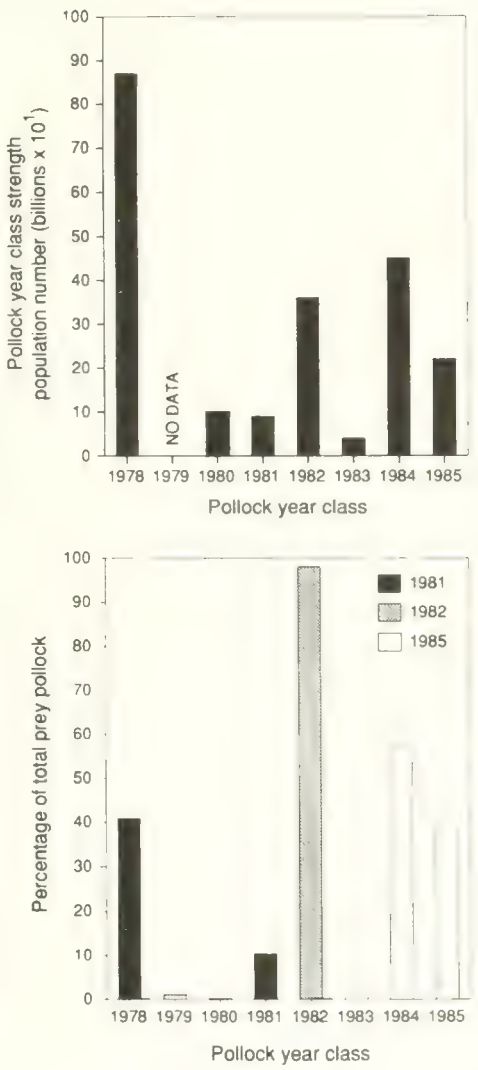

Figure 7

Estimates of walleye pollock (*Theragra chalcogramma*) year-class strength 1978–85 (Bakkala et al., 1987), and the relative abundance of specific year classes in northern fur seal gastrointestinal tracts.

is size and the tendency to form dense schools. In this sense, a "juvenation" of walleye pollock in the Bering Sea (Swartzman and Haar, 1983) may have provided fur seals with a newly abundant but unstable resource, due to large fluctuations in the annual year-class strength of walleye pollock and due to potential displacement of other prey species (Pacific herring and capelin). During years of low pollock recruitment, fur seals may switch to other prey such as capelin and Pacific herring, and experience food limitation only if these alternate prey resources have been displaced or depleted. Historical records of northern fur seal diet are inadequate to either support or refute an "alternate prey" argument. However, we suggest that when juvenile walleye pollock are unavailable, such as in our 1981 sampling season, female and juvenile fur seals select other specific prey of the same size and eat adult walleye pollock only if these other preferred prey are not available.

During their summer breeding season, northern fur seals consume the most abundant and available fish and squid in the eastern Bering Sea. Walleye pollock make up an estimated 50% of the groundfish biomass in the eastern Bering Sea and Aleutian Islands area (Walters et al., 1988) and dense aggregations of 0–age pollock occur off the Pribilof Islands June through mid-August (Smith, 1981). Kubodera and Jefferts (1984) suggested gonatids are the major pelagic cephalopod group in the Bering Sea, where large increases in abundances of larval and postlarval gonatid squid occur in early June. Among Bering Sea gonatids, *Gonatopsis borealis* and *Berryteuthis magister* are considered to be among the most numerically dominant (Jefferts, 1983; Kubodera and Jefferts, 1984).

Selection by northern fur seals of a wide variety of numerically dominant prey species throughout their migratory range has led to the general conclusion that they are non-specific, opportunistic feeders (Kajimura, 1985). Northern fur seals are flexible in their feeding habits, as indicated by the variation in GI contents of seals collected between California and Alaska. Nonetheless, fur seals concentrate on an average of three primary species within each oceanographic subregion (Perez and Bigg, 1986). In addition, fur seal consumption of walleye pollock, gonatid squid, and bathylagid smelt in the eastern Bering Sea is consistent throughout historical records, despite the wide variety of prey available to fur seals within their diving range. Based on this study, we conclude that female and young male fur seals select juvenile and small-sized fish and squid, despite the availability of larger prey types within their diving range. This study demonstrates that female and young male fur seals are size-selective midwater shelf and mesopelagic feeders, at least during the breeding and haul-out season in the eastern Bering Sea.

Acknowledgments

Otolith identifications for the 1981 samples were made by the late J. Fitch. Otolith identifications for 1982 and 1985 were based on the otolith reference collections at the National Marine Mammal Labo-

ratory (NMML) and Los Angeles County Museum (LACM). Cephalopod identifications were based on the reference collections of the NMML and Oregon State University (OSU). Voucher specimens of prey material (statoliths, beaks, otoliths, teeth, and bones) are archived at the NMML. Identifications of squid and squid beaks were confirmed by C. Fiscus (NMML, retired), K. Jefferts (OSU), and W. Walker (LACM). Identification of fish otoliths and bones were confirmed by G. Antonelis Jr. (NMML) and J. Dunn (University of Washington) respectively. Voucher samples of juvenile pollock otoliths were confirmed by A. Brown (Alaska Fisheries Science Center [AFSC]), K. Frost (Alaska Department of Fish and Game [ADF&G], and L. Lowry [ADF&G]). Gary Walters (AFSC) helped interpret bottom trawl values, and W. Carlson and C. Leap of the AFSC Graphics Unit helped produce the figures.

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Literature cited

Bailey, K., R. Francis, and J. Schumacher.
1986. Recent information on the causes of variability in recruitment of Alaska pollock in the eastern Bering Sea: physical conditions and biological interactions. Int. North Pac. Comm. Bull. 47:155–165.

Bakkala, R. G., V. G. Wespestad, and J. J. Traynor.
1987. Walleye pollock. *In* R. G. Bakkala and J. W. Balsiger (eds.), Condition of groundfish resources of the eastern Bering Sea and Aleutian Islands region in 1986, p. 11–29. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-117.

Bigg, M. A., and I. Fawcett.
1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). *In* J. R. H. Beddington, R. J. H. Beverton, and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 284–299. George Allen and Unwin Ltd., London.

Clarke, M. R.
1962. The identification of cephalopod "beaks" and the relationship between beak size and total body weight. Bull. Br. Mus. (Nat Hist.) Zool. 8:419–480.

Clarke, M. R. (ed.)
1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford, 273 p.

Dunn, J. R.
1983. Development and distribution of the young of northern smoothtongue, *Leuroglossus schmidti* (Bathylagidae), in the Northeast Pacific, with comments on the systematics of the genus *Leuroglossus* Gilbert. Fish. Bull. 81(1):23–40.

Fiscus, C. H., and H. Kajimura.
1965. Pelagic fur seal investigations, 1964. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. No. 522, 47 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE, BINC15700, Seattle, WA 98115–00700.

Fiscus, C. H., G. A. Baines, and F. Wilke.
1964. Pelagic fur seal investigations, Alaska waters, 1962. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. No. 475, 59 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BINC15700, Seattle, WA 98115–0070.

Fiscus, C. H., G. A. Baines, and H. Kajimura.
1965. Pelagic fur seal investigations, Alaska, 1963. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. No. 489, 33 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.

Fitch, J. E., and R. L. Brownell Jr.
1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. J. Fish. Res. Board Can. 25(12):2561–2574.

Fleiss, J. L.
1981. Statistical methods for rates and proportions, 2nd ed. John Wiley & Sons, 321 p.

Fowler, C. W.
1985. An evaluation of the role of entanglement in the population dynamics of northern fur seals on the Pribilof Islands. *In* R. S. Shomura and H. W. Yoshida (eds.), Proceedings of the workshop on the fate and impact of marine debris; 27–29 November 1984, Honolulu, HI., p. 291–307. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-54.

Fowler, C. W., and D. B. Siniff.
1992. Determining population status and the use of biological indices for the management of marine mammals. *In* D. R. McCullough and R. H. Reginald (eds.), Wildlife 2001: populations, p. 1051–1061. Elsevier Science Publishers. London, England.

Frost, K. J., and L. F. Lowry.
1981. Trophic importance of some marine gadids in northern Alaska and their body-otolith size relationships. Fish. Bull. 79(1):187–192.

[9] Hacker, E. S., and G. A. Antonelis Jr. 1986. Pelagic food habits of northern fur seals. *In* T. R. Loughlin and P. Livingston (eds.), Summary of joint research on the diets of northern fur seals and fish in the Bering Sea during 1985, p. 5–22. NWAFC Proc. Rep. 86–19, Alaska Fish. Sci. Cent., NMFS, NOAA, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.

Gabriel, W. L.
1978. Statistics of selectivity. *In* S. J. Lipovsky and C. A. Simenstad (eds.), Gutshop '78, p. 62–66. Wash. Sea Grant Publ. WSG-WO-77–2, Univ. Washington, Seattle, WA.

Gentry, R. L., G. L. Kooyman, and M. E. Goebel.
1986. Feeding and diving behavior of northern fur seals. *In* R. L. Gentry and G. L. Kooyman (eds.), Fur seals: maternal strategies on land and at sea, p. 61–78. Princeton Univ. Press, Princeton, NJ.

Goebel, M. E., J. L. Bengtson, R. L. DeLong, R. L. Gentry, and T. R. Loughlin.
1991. Diving patterns and foraging locations of female northern fur seals. Fish. Bull. 89:171–179.

Jefferts, K.
1983. Zoography and systematics of cephalopods of the northeastern Pacific Ocean. Ph.D. diss., Oregon State University, Corvallis, OR, 291 p.

Kajimura, H.
1984. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-779, 49 p.
1985. Opportunistic feeding by the northern fur seal, (*Callorhinus ursinus*). *In* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 300–318. George Allen and Unwin Ltd., London.

Kinder, T. H., and J. D. Schumacher.
1981. Hydrographic structure over the continental shelf of the southeastern Bering Sea. *In* D. W. Hood, and J. A. Calder (eds.), The eastern Bering Sea shelf: oceanography and resources, Vol. I, p. 31–52. Office of Mar. Poll. Assessment of NOAA.

Kubodera, T., and K. Jefferts.
1984. Distribution and abundance of the early life stages of squid, primarily Gonatidae (Cephalopoda, Oegopsida), in the northern North Pacific (Part I and II). Bull. Nat. Sci. Mus. (Tokyo) Ser. A, 10(3 and 4):91–193.

Langton R. W.
1982. Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish. Fish. Bull. 80(4):745–759.

Loughlin, T. R., J. L. Bengston, and R. L. Merrick.
1987. Characteristics of feeding trips of female northern fur seals. Can. J. Zool. 65(8):2079–2084.

Lynde, C. M.
1984. Juvenile and adult walleye pollock of the eastern Bering Sea. *In* D. Ito (ed.), Proceedings of the workshop on walleye pollock and its ecosystem in the eastern Bering Sea, p. 43–108. U. S. Dep. Commer., NOAA Tech. Memo NMFS F/NWC-62.

Mead Jr., G. W.
1953. The food habits of the North Pacific fur seal in Japanese waters. Ph.D. diss., Stanford Univ., Palo Alto, CA, 138 p.

Meek, A.
1916. The migrations of fish. Edward Arnold, London, 427 p.

Morrow, J. E.
1979. Preliminary keys to otoliths of some adult fishes of the Gulf of Alaska, Bering Sea, and Beaufort Sea. U.S. Dep. Commer. NOAA Tech. Rep. NMFS Circ. 420, 33 p.

Murie, D. J., and D. M. Lavigne.
1985. Interpretation of otoliths in stomach content analyses of phocid seals: quantifying fish consumption. Can. J. Zool. 64:1152–1157.

Nishiyama, T., K. Hirano, and T. Haryu.
1986. The early life history and feeding habits of larval walleye pollock, *Theragra chalcogramma* (Pallas), in the southeast Bering Sea. Int. North Pac. Fish. Comm. Bull. 45:177–227.

Perez, M. A., and M. A. Bigg.
1986. Diet of northern fur seals, *Callorhinus ursinus*, off western North America. Fish. Bull. 84(4):957–971.

Ponganis, P. J., R. L. Gentry, E. P. Ponganis, and K. V. Ponganis.
1992. Analysis of swim velocities during deep and shallow dives of two northern fur seals, *Callorhinus ursinus*. Mar. Mammal Sci. 8(1):69–75.

Roper, C. F. E., and R. E. Young.
1975. Vertical distribution of pelagic cephalopods. Smithson. Contrib. Zool. 209, 51 p.

Royer, T. C.
1989. Upper ocean temperature variability in the northeast Pacific Ocean: is it an indicator of global warming? J. Geophys. Res. 94(C12):18,175–18,183.

Scheffer, V. B.
1950a. The food of the Alaska fur seal. Transactions of the fifteenth North American Wildlife Conference, p. 410–420. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.
1950b. Growth layers on the teeth of Pinnipedia as an indication of age. Science 112:309–311.

Sinclair, E. H.
1988. Feeding habits of northern fur seals in the eastern Bering Sea. M.S. thesis, College of Oceanography, Oregon State Univ., 1988, Corvallis, OR, 94 p.

Smith, G. B.
1981. The biology of walleye pollock. *In* D. W. Hood and J. A. Calder (eds.), The eastern Bering Sea Shelf: oceanography and resources, Vol. I, p. 527–552. Office of Mar. Poll. Assessment of NOAA, 625 p.

Smith, G. B., and R. G. Bakkala.
1982. Demersal fish resources of the Eastern Bering Sea: spring 1976. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-754, 129 p.

Spalding, D. J.
1964. Comparative feeding habits of the fur seal, sea lion, and harbour seal on the British Columbia Coast. Fish. Res. Board Can. Bull. 146, 52 p.

Swartzman, G. L., and R. T. Haar.
1983. Interactions between fur seal populations

and fisheries in the Bering Sea. Fish. Bull. 81(1): 121–132.

Turner, L. M.

1886. Researches in Alaska. Pt. IV: Fishes. Contributions to the natural history of Alaska: results of investigations made chiefly in the Yukon district and the Aleutian Islands; conducted under the auspices of the Signal Service, U.S. Army, extending from May 1874, to August 1881, p. 87–113. No. II, Arctic Series of Publs., issued in connection with the Signal Service, U.S. Army Gov. Print. Off., Washington DC.

Wada, K.

1971. Food and feeding habit of northern fur seals along the coast of Sanriku. Bull. Tokai Reg. Fish. Res. Lab 64, Jan., p. 1–37.

Walline, P. D.

1983. Growth of larval and juvenile walleye pollock related to year-class strength. Ph.D. diss., Univ. Washington, Seattle, WA, 144 p.

Walters, G. E., K. Teshima, J. J. Traynor, R. G. Bakkala, J. A. Sassano, K. L. Halliday, W. A. Karp, K. Mito, N. J. Williamson, and D. M. Smith.

1988. Distribution, abundance, and biological characteristics of groundfish in the eastern Bering Sea based on results of the U.S.-Japan triennial bottom trawl and hydroacoustic surveys during May-September, 1985. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-154, 400 p.

Wespestad, V. G., and L. H. Barton.

1981. Distribution, migration, and status of Pacific herring. *In* D. W. Hood and J. A. Calder (eds.), The eastern Bering Sea Shelf: oceanography and resources, Vol. I, p. 509–525. Office of Mar. Poll. Assessment of NOAA, 625 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., BinC15700, Seattle, WA 98115–0070.

Wespestad, V. G., and S. M. Fried.

1983. Review of the biology and abundance trends of Pacific herring (*Clupea harengus pallasi*). *In* W. S. Wooster (ed.), From year to year, p. 17–29. Univ. Washington, Seattle, WA. Sea Grant Prog. Publ. WSG-WO-83-3.

Wilke, F., and K. W. Kenyon.

1952. Notes on the food of fur seal, sea-lion, and harbor porpoise. J. Wildl. Manage. 16(3):396–397.

1957. The food of fur seals in the eastern Bering Sea. J. Wildl. Manage. 21(2):237–238.

York, A. E.

1990. Trends in numbers of pups born on St. Paul and St. George Islands 1973–88. *In* H. Kajimura (ed.), Fur seal investigations, 1987–88, p. 31–37. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-180.

York, A. E., and J. R. Hartley.

1981. Pup production following harvest of female northern fur seals. Can. J. Fish. Aquat. Sci. 38:84–90.

York, A. E., and P. Kozloff.

1987. On the estimation of numbers of northern fur seal, *Callorhinus ursinus*, pups born on St. Paul Island, 1980–1986. Fish. Bull. 85(2):367–375.

Young R. E.

1972. The systematics and areal distribution of pelagic cephalopods from the seas off southern California. Smithson. Contrib. Zool. (97), 159 p.

Feeding habits of anadromous alewives, *Alosa pseudoharengus*, off the Atlantic Coast of Nova Scotia

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Abstract.— The stomach contents of 1,215 anadromous alewives collected during winter and summer groundfish research surveys (1990–91) off Nova Scotia were examined to 1) describe the diet by season, area, bottom depth (<101 m, 101–200 m, >200 m), time of day and fish size (<151 mm, 151–200 mm, 201–250 mm, >250 mm FL), 2) evaluate diel feeding periodicity, and 3) estimate daily ration. Euphausiids, particularly *Meganyctiphanes norvegica*, were the most important prey and represented more than 82% by volume of total stomach contents seasonally and geographically. Contributions by other prey groups (hyperiid amphipods, calanoid copepods, crustacean larvae, polychaetes, chaetognaths, mysids, pteropods, and fish larvae) were small and varied temporally and spatially. The proportion of euphausiids in the diet of alewives from the Scotian Shelf (winter) and Bay of Fundy (summer) tended to increase with increasing depth. Day and night differences in diet composition indicate that alewives may particulate-feed on macrozooplankton when prey visibility is high and filter-feed on microzooplankton when prey visibility is low. Diet composition was relatively homogenous among alewife size groups with euphausiids composing most of the total food volume. Alewives of different size groups ate similarly sized *M. norvegica*, generally the largest *M. norvegica* available. Diel feeding activity (stomach fullness) peaked at mid-day (summer collections) and mid-afternoon (winter collections); feeding activity was reduced at night. In all areas, feeding activity and the proportion of feeding fish was highest in regions where bottom depths exceeded 200 m. Mean stomach fullness was highest during summer in the Bay of Fundy and during winter on the Scotian Shelf; these regions are seasonally important foraging areas for alewives off Nova Scotia. Daily ration was 1.2% of body weight during winter and 1.9% during summer.

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The anadromous alewife, *Alosa pseudoharengus*, is a clupeiform fish whose range extends from Newfoundland to North Carolina (Bigelow and Schroeder, 1953). Off Nova Scotia, alewives occur throughout the year in regions characterized by strong tidal mixing and upwelling in the Bay of Fundy-eastern Gulf of Maine and are abundant during spring in the warmer, deeper waters of the central Scotian Shelf and areas of warm slope water intrusion along the Scotian Slope and the edges of Georges Bank (Stone and Jessop, 1992). In the Maritime provinces of Canada and Atlantic coastal United States, alewives and blueback herring, *A. aestivalis*, are fished commercially during their spring spawning migrations and are often marketed together as gaspereau or river herring. Little is known about the importance of alewives as predators in the marine environment or about their feeding habits and food consumption rates.

Alewives are generally classified as size-selective, particulate and filter-feeding microphagists and can actively feed on individual zooplankton or passively feed by filtering the water with their gill rakers (Janssen, 1976; Durbin, 1979; James, 1988). Feeding mode depends on prey density, size, and visibility, and on predator size (Janssen, 1976, 1978a, 1978b; Durbin, 1979). The ability to switch feeding modes enables alewives to consume a wide size range of prey in a variety of environmental conditions. Size-selective predation by juvenile and nonanadromous freshwater alewives can shift the species and size composition of zooplankton communities towards smaller forms (Brooks and Dodson, 1965; Brooks, 1968; Wells, 1970; Warshaw, 1972; Vigerstad and Cobb, 1978). No information is available on size-selective predation in the ocean; however, in Minas Basin, a turbid macrotidal estuary, alewives were generally particulate feeders of larger, benthic prey rather than smaller pelagic prey (Stone and Daborn, 1987).

Information on the feeding habits of anadromous alewives in the ocean is limited to qualitative assessments but is better known for freshwater juveniles (Vigerstad and Cobb, 1978; Gregory et al., 1983; Jessop, 1990) and estuarine resident subadults during summer (Stone and Daborn, 1987). Euphausiids, calanoid copepods and, to a lesser extent, hyperiid amphipods, chaetognaths, mysids, pteropods, decapod larvae, and salps

have been identified as prey for alewives in continental shelf waters from North Carolina to Nova Scotia (Holland and Yelverton, 1973; Edwards and Bowman, 1979; Neves, 1981; Vinogradov, 1984; Bowman, 1986). However, none of these studies were comprehensive.

We examined the stomach contents of anadromous alewives obtained from winter and summer groundfish research surveys on the Scotian Shelf, Georges Bank, and in the Bay of Fundy to determine the importance of these regions as foraging areas for these fish. Seasonal, spatial, diel and size-related variability in feeding are examined. Daily ration is estimated from information on diel feeding periodicity.

Materials and methods

Data collection

Alewives were collected from seven groundfish research surveys conducted by the Canadian Department of Fisheries and Oceans in three regions (Georges Bank, central Scotian Shelf, and outer Bay of Fundy) during winter (February–March) and summer (July) over a two-year period (1990–91) (Table 1). All surveys used a Western IIA bottom trawl with a 10-mm stretched-mesh liner in the cod end. Thirty-minute tows at each sampling station were conducted throughout the 24-hour day. Up to 40 fish of representative size range from each set were frozen for later analysis. Bottom water temperature (°C), time of tow deployment, latitude, longitude, and bottom depth (m) were recorded for each set. Stomach content data were grouped by season and sample location: Winter-Fundy, Winter-Shelf, Winter-Georges, and Summer-Fundy (Fig. 1). Stone and Jessop (1992) provide additional details of the survey area and procedures, and seasonal distribution of fish.

Fork length (mm), weight (g), sex and species (determined by peritoneal colour (Leim and Scott, 1966)) were recorded for each fish. Whole digestive tracts, individually identified, were preserved in 4% buffered formalin.

Diet analysis

Stomachs were weighed (±0.01 g) and the contents ranked subjectively using a fullness code (0=empty, 1=12% full, 2=25% full, 3=50% full, 4=75% full, 5=100% full) and a digestion code (1=finely digested, nothing recognizable; 2=medium digestion, some recognizable parts; 3=some digested, some undigested material; 4=undigested whole animals). The stomach content weight was obtained by subtracting the weight of the empty stomach from the total stomach weight. Stomach content weight, as a percentage of fish body weight (%BW), was used as an index of fullness to evaluate feeding activity and estimate daily ration. Stomach contents were identified (to species where possible), enumerated, and the volume of each food type estimated by means of a points system (Swynnerton and Worthington, 1940; Stone and Daborn, 1987).

For diet analysis, prey taxa (Table 2) were grouped into nine categories based on taxonomy and ecology: 1) euphausiids (*Meganyctiphanes norvegica* and some *Thysanoessa* spp.); 2) hyperiid amphipods (*Parathemisto gaudichaudi*); 3) calanoid copepods (*Calanus* spp., *Centrophages* spp. and *Metridia* spp.); 4) polychaetes (*Nereis* spp. and unidentifiable species); 5) fish larvae (*Ammodytes dubius* and unidentifiable species); 6) mysids (*Neomysis americana*); 7)

Table 1

Stomach and fork length statistics, by season and geographic area, for alewives, *Alosa pseudoharengus*, obtained from groundfish research surveys conducted off Nova Scotia (1990–1991).

	Collection date		Number			Fork length (mm)	
Season and area	1990	1991	Sets	Stomachs	Stomachs with prey	Mean ± SD	Range
Winter-Fundy	2–10 Feb	—	9	112	58	201.9 ± 5.38	100–303
Winter-Georges	28 Feb–Mar 7	Feb 16–26	29	438	147	193.6 ± 1.83	118–305
Winter-Shelf	13–19 Mar	Mar 15–18	29	489	322	223.8 ± 2.82	95–302
Summer-Fundy	6–10 Jul	Jul 05–09	15	176	141	242.6 ± 2.48	142–302
Total			82	1,215	668	213.6 ± 1.86	95–305

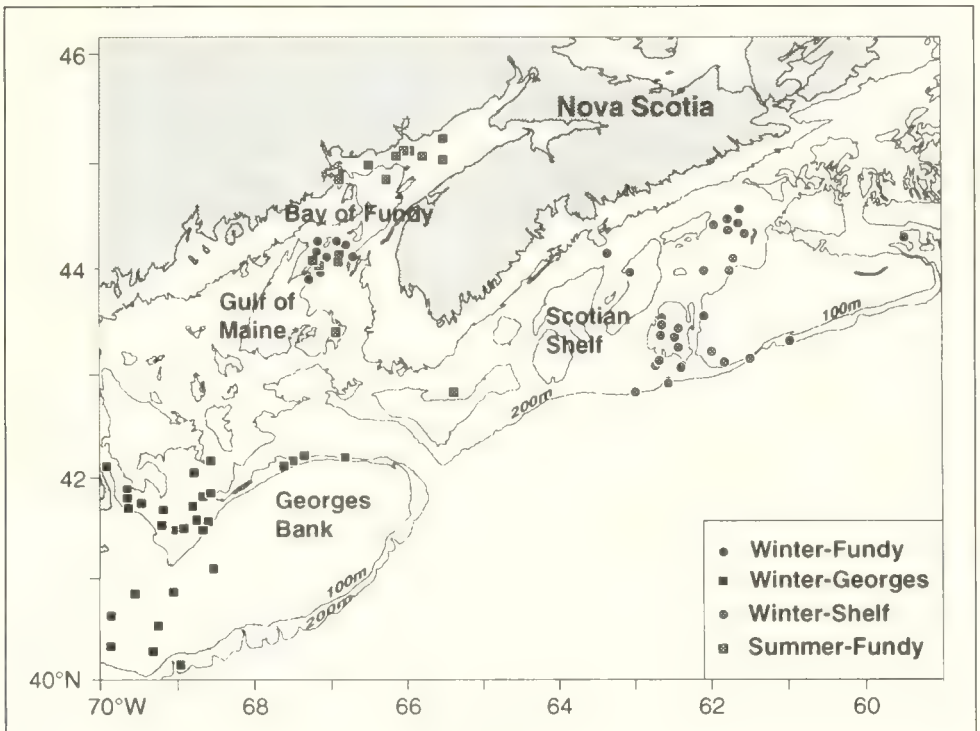

Figure 1

Set locations for alewives, *Alosa pseudoharengus*, obtained from groundfish research surveys off the Atlantic coast of Nova Scotia (1990–91) grouped by season and geographic area. Offshore banks are delineated by the 100-m depth contour; the outer edge of the continental shelf is delineated by the 200-m depth contour.

chaetognaths; 8) crustacean larvae (furciliae of *Thysanoessa* spp. and some decapod larvae); and 9) pteropods. The percent frequency of occurrence (%FO), percent of total stomach content number (%N), and percent of total stomach content volume (%V) of prey categories were estimated for stomachs containing recognizable food (digestion code ≥2). The Index of Relative Importance (IRI=(%N+%V) x %FO) was calculated for each prey category (Pinkas et al., 1971) and used for various diet comparisons. Diets were analyzed by season and geographic area (Winter-Fundy, Winter-Georges, Winter-Shelf, Summer-Fundy), as well as by depth range within season and area, to compare food items from shallow regions and offshore banks (<100 m), mid-depths (101–200 m) and the shelf edge or deep basins (>200 m). Diel differences in diet composition (day and night, based on time of gear deployment) were examined for the entire data set. Ontogenetic differences in diet within season/area were examined by grouping fish lengths into four size classes (<151, 151–200, 201–250 and >250 mm FL), which were assumed sufficient for detecting shifts in prey composition. Data from 1990 and 1991 were combined for all comparisons because the ranks of IRI values for all prey categories between years were highly correlated (Spearman rank correlation coefficient (r_s)=0.67; P<0.05; n=9).

Predator-prey size analysis

Total lengths (±1 mm, tip of rostrum to end of telson) of undigested, whole *M. norvegica* in the stomachs of 55 alewives (>200 mm FL, since most intact prey occurred only in larger fish) from Winter-Georges, Winter-Shelf, and Summer-Fundy cruises were compared with predator size. *Thysanoessa* spp. were not measured because of poor condition. Lengths of *M. norvegica* from Emerald Basin collected in June 1991, by Sameoto et al. (1993) using the Bedford Institute of Oceanography Net and Environmental Sensing System (BIONESS) were compared with euphausiid length frequencies from stomach contents to estimate the proportion of the available size range of *M. norvegica* consumed by alewives. The BIONESS is not considered to be size-selective for euphausiids (Sameoto et al., 1980).

Diel feeding periodicity and daily ration estimate

Diel feeding periodicity and daily ration were examined separately for winter (Bay of Fundy, Scotian Shelf, and Georges Bank combined) and summer (Bay of Fundy) collections because of seasonal differences in photoperiod. Stomach fullness data from tows within each successive 3–hour (winter cruises) and 4–hour (summer cruises) interval were grouped and assigned to the midpoint of the time period. Small sample sizes precluded grouping of summer collections into 3–hour intervals.

Daily ration (DR) of alewives during winter and summer and by size class during winter (<151 mm, 151–200 mm, 201–250 mm, >250 mm) was estimated in terms of % body weight from the model of Elliott and Persson (1978):

$$C_t = \frac{\left(S_t - S_0 e^{-Rt}\right)}{1 - e^{-Rt}} Rt;$$

where the consumption of food (C_t) during the time interval t_0 to t_t is calculated from the average amount of food in the stomach at time t_0 (S_0), the amount in the stomach at time t_t (S_t) and the instantaneous evacuation rate R. The estimates of C_t calculated for each time interval are then summed to give the total daily ration (DR). Feeding is assumed constant within each time interval. R is assumed exponential and temperature dependent (Elliott, 1972), as

$$R = ae^{bT}.$$

The slope (b) may be fairly constant for different prey types and fish species (mean=0.115), but the intercept (a) changes with prey type and can be estimated from gastric evacuation experiments (Durbin et al., 1983). Gastric evacuation rate data are unavailable for anadromous alewives; therefore, an intercept (a=0.0406) was obtained from Durbin et al. (1983) based on values for a variety of small invertebrates fed to several freshwater and marine fishes. High fat levels in the prey may retard evacuation (Durbin et al., 1983) but the principal food item in this study (*M. norvegica*) has a low lipid content (Ackman et al., 1970). Average bottom temperatures for winter (mean=7.16°C) and summer (mean=7.43°C) collections were used to estimate R.

Statistical analysis

Differences in the rankings of IRI values for prey categories (n =8) between three or more groups were tested for significance with the Kendall coefficient of concordance (w) (Siegel, 1956); for paired groups, the Spearman rank correlation coefficient (r_s) was used (Fritz, 1974). Euphausiids, which consistently ranked highest in importance in all comparisons, were excluded from correlation analysis to reduce bias and emphasize correlations among remaining prey groups.

One-way ANOVA was used to examine feeding activity, represented by the index of fullness (arcsine $\sqrt{p}$ transformed) by season and geographic area, by depth range within season and geographic area and by diel sampling period (winter and summer collections) and to compare total lengths of euphausiid prey. Paired means, adjusted for unequal sample sizes, were compared with the Tukey-Kramer test (Sokal and Rohlf, 1981). The relation between predator fork length and mean prey length was examined by linear regression for alewives with three or more *M. norvegica* present in their stomachs.

Results

Alewives examined for stomach contents measured 95 to 305 mm FL (mean=213.6 mm, n=1,215); fish from summer cruises in the Bay of Fundy were larger on average than those from other collections (Table 1). Capture depths ranged from 36 to 269 m, although most (75%) specimens were obtained from regions 101 to 200 m deep.

Recognizable prey from over 20 different taxa occurred in 55% (668 of 1,215) of stomachs examined (Table 2). Over 95% of the total prey number, volume, and frequency of occurrence were crustaceans (Table 2). Euphausiids were the most prevalent (91% by volume); *Meganyctiphanes norvegica* were dominant by volume (61%) and furcilia larvae of *Thysanoessa* spp. were dominant numerically (32%). Other prey, including hyperiid amphipods, calanoid copepods, crustacean larvae, mysids, polychaetes, chaetognaths, pteropods, and fish larvae contributed little and varied temporally and spatially in relative importance.

Diet composition by season and area

Euphausiids were the most important food of alewives during winter and summer for all areas (Fig. 2). During winter, alewives from the outer Bay of Fundy and Georges Bank fed almost exclusively on euphausiids (99% and 95% of total volume, respectively). On Georges Bank, small (%V≤3) proportions of calanoid copepods, hyperiid amphipods, and pteropods were also consumed. Prey diversity was greatest for alewives from the Scotian Shelf; euphausiids dominated by volume (82%) but were numeri-

Table 2

Prey items found in the stomachs of alewives, *Alosa pseudoharengus*, collected from groundfish research surveys off Nova Scotia, 1990–91. %FO = percent frequency of occurrence, %N = percent by number, %V = percent by volume.

Prey item	%FO	%N	%V	Prey item	%FO	%N	%V
Crustacea	97.6	95.0	97.3	Decapoda	0.5	0.1	<0.1
Euphausiacea	91.3	72.4	91.0	Zoea	0.2	<0.1	<0.1
Meganyctiphanes norvegica	37.7	29.4	60.9	Megalopa	0.3	0.1	<0.1
Thysanoessa spp	6.9	4.5	6.0	Cirripedia Cypris larvae	0.2	<0.1	<0.1
Thysanoessa spp furcillia	3.7	32.1	1.2				
Unidentified Euphausiacea	40.1	6.3	23.0	Insecta Hymenoptera	0.5	<0.1	<0.1
				Polychaeta	1.8	0.1	0.5
Amphipoda	15.9	4.7	4.8	*Nereis* spp	1.1	0.1	0.4
Hyperiidea	15.6	4.2	4.4	Unidentified Polychaeta	0.8	<0.1	0.1
Parathemisto gaudichaudi	9.9	3.1	2.9				
Unidentified Hyperiidea	5.7	1.0	1.5	Chaetognatha	1.1	3.6	<0.5
Gammaridea	0.3	0.5	0.4				
Caprellidea	0.2	<0.1	<0.1	Hydrozoa	0.3	—	<0.1
				Gastropoda Pteropoda (*Limacina*)	5.1	0.8	0.3
Copepoda	8.2	17.4	1.2				
Calanoidea				Teleost larvae	3.9	0.5	1.4
Centrophages spp	3.1	1.3	0.2	*Ammodytes dubius*	2.7	0.5	1.0
Calanus spp	0.5	0.7	<0.1	Unidentified fish larvae	1.2	<0.1	0.4
Metridia spp	2.0	1.1	<0.1				
Unidentified calanoids	6.9	14.3	0.9	Algae	1.2	—	0.2
				Organic material	0.6	—	<0.1
Mysidacea				Unidentified remains	6.6	—	0.8
Neomysis americana	0.2	0.4	0.2				
				Total stomachs with food	668		
				Total prey number	14,752		
Cumacea	0.3	<0.1	<0.1	Total prey volume (points)	25,232		

cally less than in other areas. Hyperiid amphipods, (*Parathemisto gaudichaudi*), ranked second in importance (%V=10), followed by crustacean larvae (furciliae), calanoid copepods, and fish larvae, (*Ammodytes dubius*). During summer in the Bay of Fundy, alewives fed heavily on euphausiids (%V=95) but also consumed chaetognaths, mysids, and polychaetes (second, third, and fourth in importance).

Rankings of IRI values (excluding euphausiids) for Winter-Georges, Winter-Shelf, and Summer-Fundy samples were not significantly correlated (w=0.22, P=0.701), indicating seasonal and geographic differences in the dietary importance of these lesser prey categories. Winter-Fundy samples contained too few prey categories to be analyzed.

Diet composition by depth range

For Winter-Shelf and Summer-Fundy collections, the proportion of euphausiids in the diet increased with increasing depth (Fig. 3). At bottom depths less than 101 m on the Scotian Shelf, euphausiids composed 64% of total volume and 22% of total number; at 101 to 200 m, %V = 83 and %N = 23 and at depths greater than 200 m, %V = 96 and %N = 95. During summer in the Bay of Fundy, euphausiid consumption increased with depth such that at less than 101 m, %V = 82 and %N = 35; at 101 to 200 m, %V = 97 and %N = 97; while at depths greater than 200 m, both %V and %N = 100. Other prey categories generally decreased in number with increasing depth as did their relative proportion. For both Winter-Shelf and Summer-Fundy collections, prey diversity and abundance were greatest where bottom depths were less than 101 m.

Multiple correlations of IRI values for prey categories (excluding euphausiids) between the three bottom-depth interval groups were not significant (w=0.54, P=0.12) for Scotian Shelf collections and reflect the decreasing number of prey categories with increasing depth. For Summer-Fundy samples, the Spearman rank correlation of IRI values for the two shallower depth-intervals was not significant (r_s=-0.35, P>0.05) and euphausiids were the only prey at depths greater than 200 m.

Depth-related differences did not occur in the euphausiid-dominated diet of alewives from the Winter-Fundy and Winter-Georges collections at

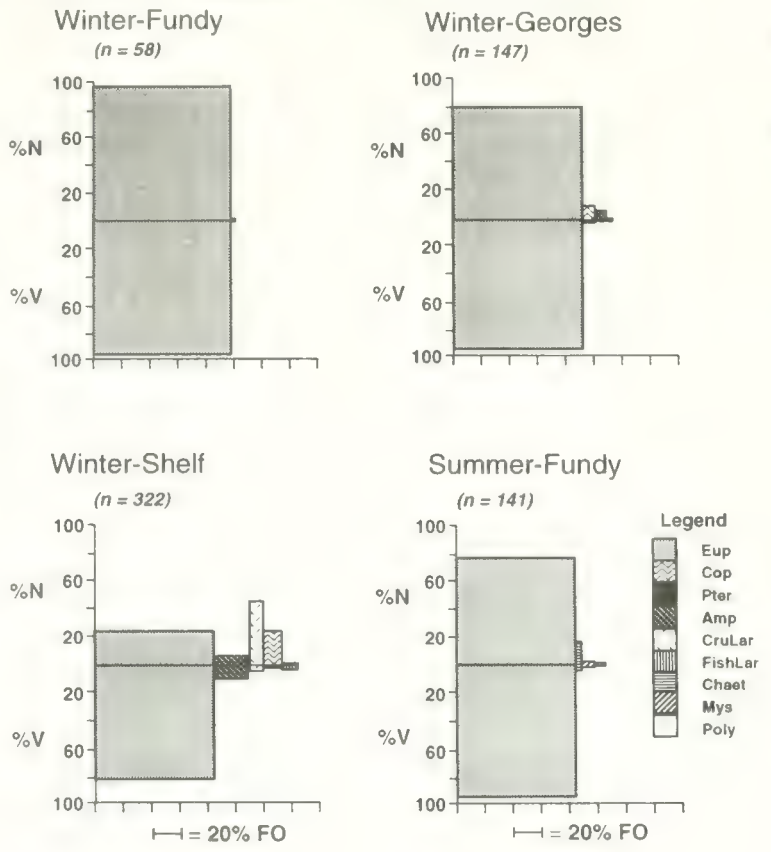

Figure 2

Relative importance of prey categories in the diet of alewives, *Alosa pseudoharengus*, collected from groundfish research surveys off Nova Scotia (1990–91), ranked from highest Index of Relative Importance (left to right) by season and area. *n* = number of stomachs with prey; %FO = % frequency of occurrence; %N = % of total prey number; %V = % of total prey volume; Eup = euphausiids; Cop = calanoid copepods; Pter = pteropods; Amp = hyperiid amphipods; CruLar = crustacean larvae; FishLar = fish larvae; Chaet = chaetognaths; Mys = mysids; Poly = polychaetes.

bottom depths exceeding 101 m (no fish were obtained at bottom depths less than 101 m). IRI rankings of prey categories between depth groups [illegible] correlated present for analysis of Winter-Fundy collections. In both winter and summer, most euphausiids consumed at depths less than 101 m were *Thysanoessa* [illegible] and [illegible] for shallower regions (Table 3).

Diel variation in the diet

[illegible] stomachs [illegible] tions, higher numbers and volumes were ingested during the day (%N=74, %V=92) than at night (%N=16, %V=85) (Fig. 4). IRI values for day and night collections were not significantly correlated (r_s=0.26, P>0.05) reflecting the greater consumption of hyperiid amphipods during the day and copepods, crustacean larvae and fish larvae at night.

Diet composition by size class

Diet composition was relatively homogeneous among alewife size groups (<151 mm, 151–200 mm, 201–250 mm, >250 mm) with euphausiids composing most of the total food volume (Fig. 5). Multiple correlations of IRI values for prey categories (excluding euphausiids) by fish length group were significant for both the Scotian Shelf (w=0.58, P=0.024) and Georges Bank (w=0.65, P=0.011). For Summer-Fundy collections, diets of the two largest size groups were nearly identical; IRI values were not significantly correlated (r_s=0.38, P>0.05) due to slight differences in the rankings of minor prey categories (i.e., amphipods, mysids, polychaetes, chaetognaths).

Prey size composition

Alewives ingested similar sizes of *M. norvegica* during winter (Georges Bank, Scotian Shelf) and summer (Bay of Fundy) (Fig. 6). Modal peaks in euphausiid size appeared at 25–27 mm and 30 mm on the Scotian Shelf and at 30–35 mm for Georges Bank and the Bay of Fundy. In comparison, *M. norvegica* from Emerald Basin BIONESS collections in June 1991 were bimodally [illegible] at 25–27 mm and 34 mm. Euphausiids larger than 29 mm were proportionately less frequent than in stomach contents.

Mean lengths of *M. norvegica* consumed by alewives varied by season/area group ($F_{2,701}$=65.5, P<0.001), although differences between means were small (Winter-Georges: mean=32.1±3.13; Winter-Shelf: mean=28.7±3.72; Summer-Fundy: mean =31.2±3.64). The average size of euphausiids consumed did not differ ($F_{1,50}$=3.31, P =0.075) with alewife size range 225–300 mm FL.

Feeding activity

Feeding activity, as indicated by mean stomach fullness index values, varied by season/geographic area ($F_{3,1210}$=46.20, P< 0.001). Mean stomach fullness was highest for Summer-Fundy and Winter-Shelf collections and lowest for Winter-Fundy and Winter-Georges collections (Table 4). The proportion of feeding fish was highest during summer in the Bay of Fundy (80.6%) and lowest during winter on Georges Bank (33.6%). Stomach fullness was significantly higher at bottom depths greater than 200 m for all but the Winter-Shelf collections, where mean fullness did not differ among depth groups (Table 4). Similarly, the proportion of feeding fish was highest in areas exceeding 200 m deep for all collections.

Alewife feeding activity varied throughout the diel period during winter ($F_{7,1031}$=24.97, P< 0.001) and summer ($F_{5,196}$= 7.98, P<0.001) with maximum fullness in both seasons occurring near mid-day (Fig. 7). In winter, feeding activity was extremely variable: mean fullness was high during early morning (0001–0430 hours), declined until dawn (0730), increased sharply until early afternoon (1330), declined again in late afternoon (1630) and then increased after sunset before falling off again prior to midnight. During summer, diel feeding activity was much more constant, although sample sizes were smaller and stomach fullness more variable. Feeding activity increased gradually after sunrise, peaked by mid-morning (1000), then declined throughout the afternoon and evening until just prior to midnight (2200). Although alewives fed actively at night during winter, peak feeding generally occurred during the day in winter and summer.

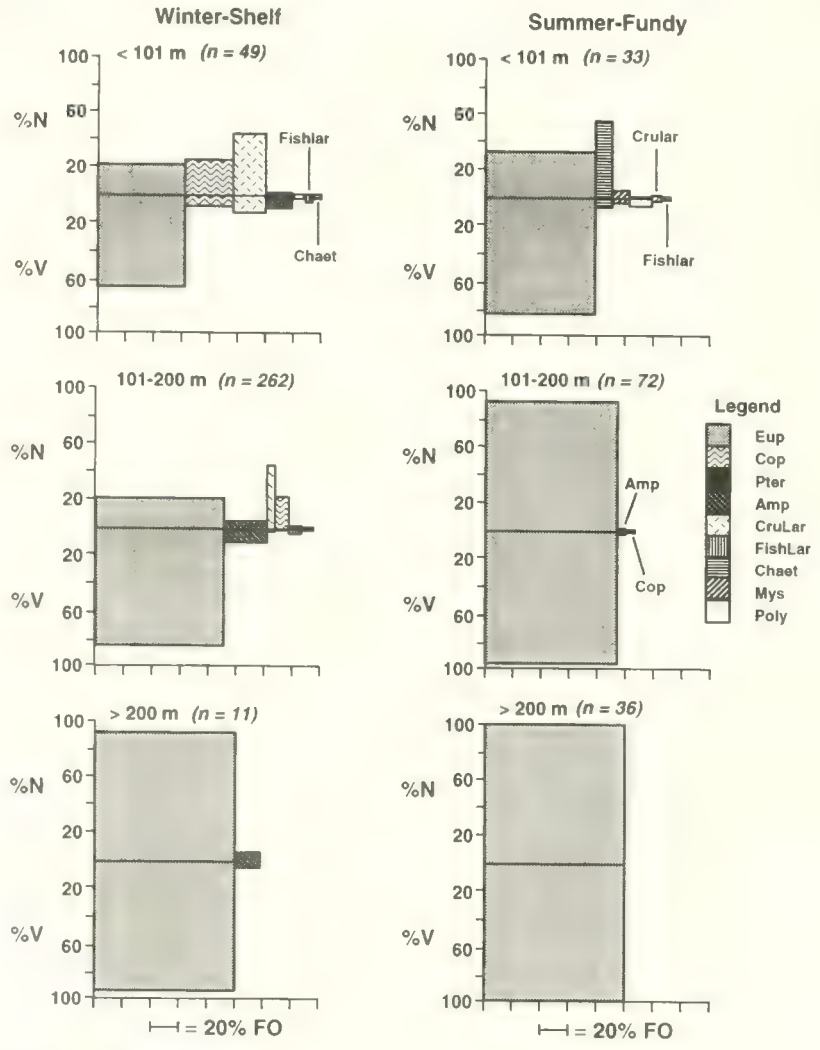

Figure 3

Relative importance of prey categories in the diet of alewives, *Alosa pseudoharengus*, obtained from groundfish research surveys off Nova Scotia (1990–91), ranked from highest Index of Relative Importance (left to right), by depth range, for Scotian Shelf (winter) and Bay of Fundy (summer) collections. (Symbols as in Fig. 2).

Daily ration

Daily consumption of alewives in the field was about 1.22% BW at 7.16°C during winter and 1.88% BW at 7.43°C during summer (Table 5). The winter daily ration of alewives generally decreased from 1.95% BW for fish less than 151 mm FL to 1.13% BW at 151–200 mm FL, 1.19% BW at 201–200 mm FL and 1.00% BW at larger than 250 mm FL.

Discussion

Our study clearly indicates that alewives off Nova Scotia feed primarily on euphausiids, particularly *Meganyctiphanes norvegica;* much smaller contributions are made by other prey. Alewives from the

Table 3

Mean number of *Meganyctiphanes norvegica* and *Thysanoessa* spp. in the stomachs of alewives, *Alosa pseudoharengus*, by depth interval within season and geographic area from groundfish research surveys off Nova Scotia (1990–91). n = number of stomachs with prey.

Season and area	Depth (m)	*M. norvegica* Mean	±	SD	n	*Thysanoessa* spp Mean	±	SD	n
Winter–Fundy	101–200	11.3	±	7.36	3	5.4	±	0.81	5
	>200	10.2	±	2.20	9	2.5	±	1.50	2
Winter–Georges	101–200	5.9	±	0.81	26	11.8	±	6.55	6
	>200	20.3	±	1.68	28	—		—	—
Winter–Shelf	<101	—		—	—	32.0	±	14.63	10
	101–200	14.7	±	1.41	89	9.6	±	3.79	20
	>200	5.8	±	3.47	4	—		—	—
Summer–Fundy	<101	18.9	±	3.47	14	12.0	±	2.00	2
	101–200	21.9	±	2.67	48	—		—	—
	>200	27.5	±	2.39	31	23.0		—	1

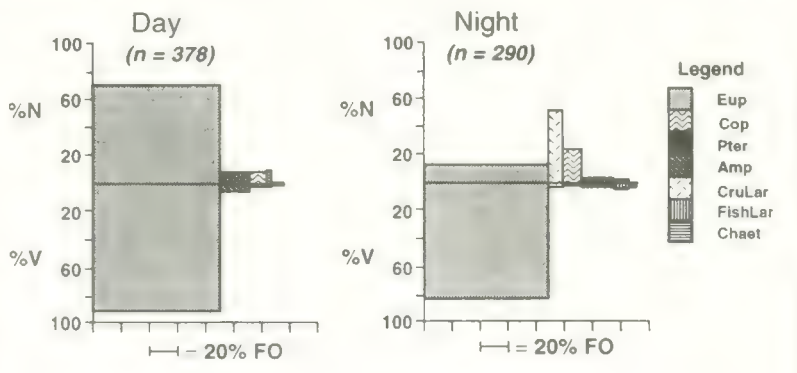

Figure 4

Relative importance of prey categories in the diet of alewives, *Alosa pseudoharengus*, obtained from groundfish research surveys off Nova Scotia (1990–91), ranked from highest Index of Relative Importance (left to right) for day and night collections (Symbols as in Fig. 2).

Atlantic seaboard of the United States consumed relatively fewer euphausiids (37–56% by weight) (Edwards and Bowman, 1979; Vinogradov, 1984) than off Nova Scotia (82–99% by volume).

Euphausiids represent a large component of the marine zooplankton community and are abundant in the Bay of Fundy (Kulka et al., 1982; Locke and Corey, 1988), Gulf of Maine (Bigelow, 1926), the deep basins of the Scotian Shelf (Herman et al., 1991) and the outer shelf and shelf slope (Sameoto, 1982). Given their two-year life cycle (Hollingshead and Corey, 1974; Berkes, 1976), the availability and relative abundance of euphausiids is more seasonally stable than for other prey species (i.e., chaetognaths, hyperiid amphipods, calanoid copepods, mysids), most of which undergo fluctuations in abundance progressing from a spring low to a summer high before declining in fall and winter (Evans, 1968; Sherman and Schaner, 1968; Corey, 1988; McLaren et al., 1989).

Small seasonal differences in diet composition reflect the opportunistic foraging behaviour of alewives and the availability of food types from offshore regions during winter as compared with the Bay of Fundy in summer. During winter, the diet diversity of alewives was greatest on the Scotian Shelf probably because the late winter (mid-March) sampling period coincides with the hatching and occurrence of the larval forms of *Thysanoessa* spp. (Berkes, 1976) and *Ammodytes dubius* (Scott, 1972), both of which occurred only in the diet of alewives from the Scotian Shelf. In the Bay of Fundy, alewife consumption of chaetognaths and mysids in the summer reflects their increased abundance and availability (Sherman and Schaner, 1968; Corey, 1988).

The increased proportion of euphausiids in the diet of alewives from the Scotian Shelf (winter) and the Bay of Fundy (summer) coincides with an increased relative abundance of euphausiids with increasing depth. In the Scotian Shelf Basins, *M. norvegica* occur between 170 m and the bottom with highest concentrations generally below 200 m (Sameoto et al., 1993). In the Bay of Fundy, *M. norvegica* is most abundant where bottom depths are between 165 and 200 m, while *Thysanoessa inermis* occur between 95 and 155 m (Kulka et al., 1982). The greater proportion and number of other prey categories at depths less than 101 m on the Scotian Shelf and in the Bay of Fundy likely result from decreased euphausiid abundance (thereby increasing the relative contribution of other prey) rather than an absolute increase in the abundance of other zooplankters. Depth-related variation in

euphausiid species composition in the diet of alewives from all regions matches differences in the bottom depth preferences of *M. norvegica* (>150 m) and *Thysanoessa* spp. (100–150 m) (Berkes, 1976; Kulka et al., 1982; Sameoto et al., 1993).

Diel differences in the diet of alewives may reflect the influence of varying light intensity on prey availability and on their relative success in locating and capturing prey. Consumption of microzooplankters (crustacean larvae, calanoid copepods) was greater at night perhaps because of increased filter-feeding activity (Janssen, 1978b). Conversely, ingestion of macrozooplankters (euphausiids, hyperiid amphipods) may be highest during the day because visual cues favour a particulate-feeding mode.

Large size, darkly pigmented eyes, and a habit of forming large concentrations (Mauchline and Fisher, 1969) may make *M. norvegica* easily detectable by alewives during daylight whereas at night, photophores along the abdomen of *M. norvegica* may assist detection. Most euphausiid species migrate vertically over the diel period, rising from deep water (150–200 m) towards the surface at dusk, remaining near surface throughout the night, and then migrating to the depths at dawn (Mauchline, 1984). Alewives also have a diel pattern of vertical migration in the marine environment (Neves, 1981; Stone and Jessop, 1992) and may encounter sufficient light higher in the water column at night to particulate feed on euphausiids.

Ontogenetic differences in diet composition were not apparent; euphausiids dominated the diet of alewives ranging in length from 95 to 305 mm. Alewives switch from feeding primarily on microzooplankton to macrozooplankton at some point during their marine development and like other similarly sized clupeids, concentrate their feeding at intermediate trophic levels (James, 1988).

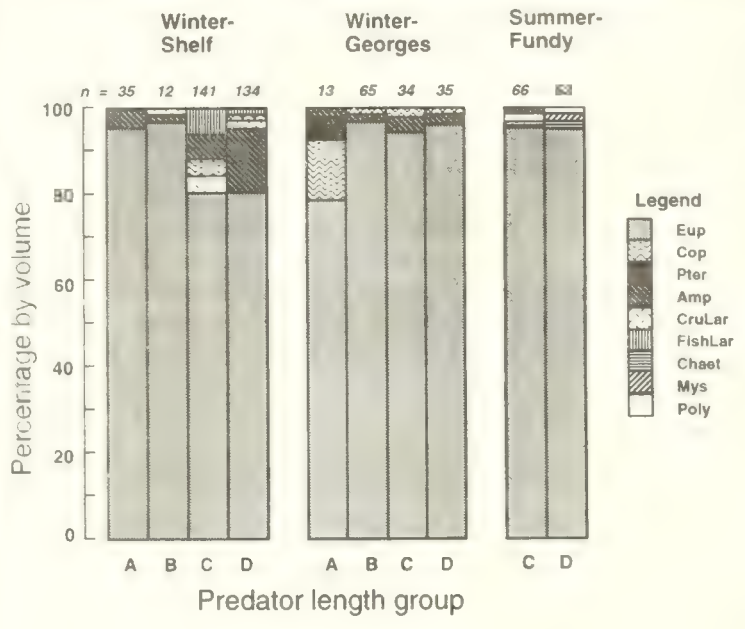

Figure 5

Percentage of total volume of prey categories in the diet of alewives, *Alosa pseudoharengus*, for different size classes (mm FL) obtained from groundfish research surveys off Nova Scotia (1990–91). Euphausiids were the only prey category in Winter-Fundy cruises. A: <151 mm; B: 151–200 mm; C: 201–250 mm; D: >250 mm; Eup = euphausiids; Cop = calanoid copepods; Pter = pteropods; Amp = hyperiid amphipods; CruLar = crustacean larvae; FishLar = fish larvae; Chaet = chaetognaths; Mys = mysids; Poly = polychaetes; *n* = number of stomachs with food.

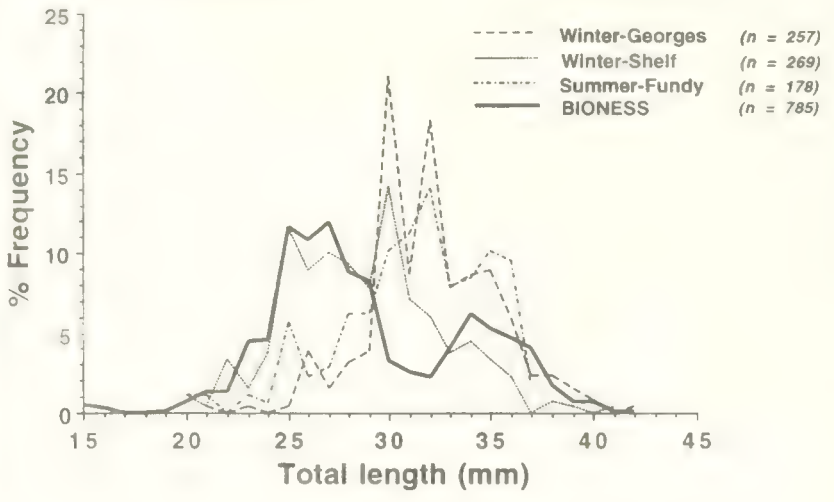

Figure 6

Size frequency distributions of *M. norvegica* consumed by alewives, *Alosa pseudoharengus*, obtained from winter (Georges Bank, Scotian Shelf) and summer (Bay of Fundy) groundfish surveys off Nova Scotia (1990–91) and from BIONESS samples in Emerald Basin (Spring, 1991). *n* = sample size.

Table 4

Mean stomach fullness index (arcsine √p transformed) by season and geographic area and by depth interval for alewives, *Alosa pseudoharengus*, obtained from groundfish research surveys off Nova Scotia (1990–91). Mean fullness index values lacking a letter in common are significantly different (Tukey HSD, $P<0.05$). n = number of stomachs examined (including empty stomachs).

Season and area	Depth (m)	n	% with food	Fullness index (%BW) Mean ± SD	Maximum
Winter–Fundy	all	112	51.8	2.3z ± 0.25	9.9
Winter–Georges	all	438	33.6	2.1z ± 0.13	9.9
Winter–Shelf	all	489	65.0	3.8y ± 0.10	10.0
Summer–Fundy	all	175	80.6	3.9y ± 0.21	10.0
Winter–Fundy	101–200	60	28.3	1.5z ± 0.29	9.4
	>200	52	78.8	3.7y ± 0.32	9.9
Winter–Georges	<101	7	28.6	2.1z ± 0.87	5.9
	101–200	376	28.7	1.7z ± 0.12	9.9
	>200	55	67.3	4.6y ± 0.46	9.9
Winter–Shelf	<101	92	55.3	3.4z ± 0.16	7.4
	101–200	385	68.1	3.9z ± 0.12	10.0
	>200	12	91.7	3.4z ± 0.46	8.0
Summer–Fundy	<101	48	68.8	3.5z ± 0.33	8.8
	101–200	87	82.8	3.6z ± 0.30	10.0
	>200	40	90.1	5.0y ± 0.51	9.8

Gilmurray (1980) found mainly microplanktonic prey (e.g., calanoid copepods, cypris larvae, insects) in the diet of alewives less than 80 mm FL obtained from tidal creeks in the upper Bay of Fundy. The shift towards consumption of macrozooplankton likely occurs at fish sizes smaller than those examined in the present study (i.e., <95 mm FL).

Diel feeding activity during winter and summer, as indicated by the mean fullness index, reached a maximum near mid-day and is typical of size-selective predators which rely on visual cues (Eggers, 1977). Summer resident subadult alewives in Minas Basin display a similar feeding pattern, although peak feeding occurred later in the afternoon (1500 hours), coincident with the time of high tide when turbidity was lowest and prey visibility highest (Stone, 1985). Summer feeding activity by juvenile anadromous alewives in freshwater also peaks during the day but ceases or declines overnight (Jessop, 1990). Nocturnal feeding by alewives was more apparent during winter than summer; the significance of this seasonal difference in feeding activity is unclear. Alewives can and do feed efficiently at night using both particulate (Janssen and Brandt, 1978) and filter-feeding (Janssen, 1978b) modes.

Alewives greater than 200 mm FL generally consumed the largest *Meganyctiphanes* available. Length-frequency distributions of *M. norvegica*, which has a life span of about two years, are typically bimodal (Hollingshead and Corey, 1974; Berkes, 1976). Alewives selectively favor larger prey (Brooks and Dodson, 1965; Brooks, 1968; Wells, 1970) and likely use a particulate feeding strategy in doing so. Slight seasonal and geographic differences in the average size of *M. norvegica* ingested likely reflect size differences in euphausiid populations rather than selection by the predator.

Daily ration calculations were based on the model of Elliott and Persson (1978) which was originally intended for field samples collected within a given area from the same population over time. Our stomach fullness data for alewives from the Bay of Fundy, Georges Bank, and the Scotian Shelf covered a wide area geographically and may involve more than one population. The broad temporal and spatial coverage reduces the effect of day-to-day and regional variations in diet which would arise from more restricted sampling. Calculated daily ration levels for alewives off Nova Scotia were similar to those reported for other teleosts (Fange and Grove, 1979). Lower estimates were obtained during winter (1.22% BW at 7.16°C) than for summer (1.88% BW at 7.43°C) since temperature is related to metabolic requirements and to the evacuation rate of stomach contents (Durbin et al., 1983). Both estimates are well above maintenance ration levels for temperatures in the 7–8°C range and are sufficient for positive growth (Brett and Groves, 1979). Alewife daily ration declined with increasing fish size; small fish, including marine species such as North Sea cod, *Gadus morhua* (Daan, 1973), winter flounder, *Pseudopleuronectes americanus* (Huebner and Langton, 1982) and silver hake, *Merluccius bilinnearis* (Durbin et al., 1983), generally consume proportionally more food per unit weight than large fish (Windell, 1978). Overall, our estimates of daily

Table 5

Mean amount of food (%BW) in the stomachs of alewives, *Alosa pseudoharengus*, obtained from groundfish surveys off Nova Scotia (1990–91), with estimates of food consumption (C_t) and daily ration ($DR = \Sigma C_t$), by season and size class. n = number of stomachs examined (including empty stomachs. For winter collections, $R = 0.0925$, temperature = 7.16°C; for summer collections, $R = 0.0954$, temperature = 7.43°C.

Season (size class)	Time period (hr)	n	Stomach contents (%BW) Mean ± SD	C_t (%BW)	DR (%BW)
Winter (all)	2400–0300	84	0.75 ± 0.100		1.216
	0300–0600	184	0.65 ± 0.053	0.098	
	0600–0900	97	0.23 ± 0.038	–0.308	
	0900–1200	122	0.52 ± 0.079	0.401	
	1200–1500	96	1.09 ± 0.104	0.792	
	1500–1800	150	0.20 ± 0.032	–0.709	
	1800–2100	177	0.52 ± 0.043	0.421	
	2100–2400	189	0.42 ± 0.053	0.033	
				0.488	
Summer (all)	2400–0400	11	0.22 ± 0.041		1.880
	0400–0800	5	0.58 ± 0.198	0.515	
	0800–1200	61	2.32 ± 0.161	2.316	
	1200–1600	74	1.32 ± 0.190	–0.320	
	1600–2000	19	0.48 ± 0.249	–0.508	
	2000–2400	5	0.03 ± 0.031	–0.357	
				0.234	
Winter (<151 mm FL)	2400–0400	29	0.95 ± 0.233		1.949
	0400–0800	31	1.13 ± 0.146	0.563	
	0800–1200	4	0.90 ± 0.382	0.143	
	1200–1600	3	1.32 ± 0.439	0.842	
	1600–2000	13	0.42 ± 0.110	–0.593	
	2000–2400	87	0.55 ± 0.103	0.311	
Winter (151–200 mm FL)	2400–0300	22	1.10 ± 0.199		1.126
	0300–0600	48	0.61 ± 0.095	–0.253	
	0600–0900	26	0.12 ± 0.048	–0.396	
	0900–1200	29	0.22 ± 0.063	0.151	
	1200–1500	9	0.84 ± 0.532	0.765	
	1500–1800	69	0.14 ± 0.039	–0.565	
	1800–2100	26	0.74 ± 0.153	0.719	
	2100–2400	25	0.16 ± 0.053	–0.457	
Winter (201–250 mm FL)	2400–0300	30	0.52 ± 0.094		1.189
	0300–0600	60	0.62 ± 0.093	0.256	
	0600–0900	23	0.27 ± 0.062	–0.222	
	0900–1200	51	0.53 ± 0.123	0.372	
	1200–1500	27	0.93 ± 0.192	0.600	
	1500–1800	56	0.31 ± 0.065	–0.453	
	1800–2100	42	0.61 ± 0.075	0.434	
	2100–2400	36	0.50 ± 0.093	0.046	
				0.156	
Winter (>250 mm FL)	2400–0300	14	0.24 ± 0.052		1.000
	0300–0600	34	0.32 ± 0.042	0.161	
	0600–0900	47	0.27 ± 0.067	0.029	
	0900–1200	39	0.68 ± 0.173	0.545	
	1200–1500	57	1.19 ± 0.124	0.772	
	1500–1800	22	0.11 ± 0.032	–0.902	
	1800–2100	39	0.31 ± 0.076	0.257	
	2100–2400	11	0.50 ± 0.141	0.302	

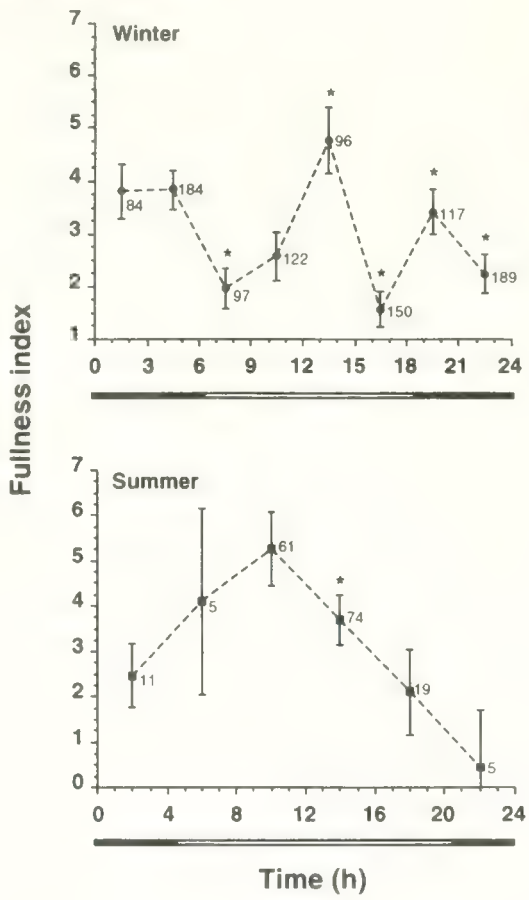

Figure 7

Diel feeding chronology of alewives, *Alosa pseudoharengus*, from winter and summer groundfish research surveys off Nova Scotia (1990–91), as determined from changes in fullness index values. Data are means (arcsine √p transformed with 95% confidence intervals) placed at the midpoint of each 3–hour (winter) and 4–hour (summer) interval. Asterisk denotes mean significantly different ($P<0.05$) from that of previous time interval. Sample size is adjacent to each symbol. Open and solid portions of horizontal bars represent light and dark hours during winter and summer.

ration may be on the low side because of possible weight loss in *M. norvegica* due to the effects of formalin preservation (Steedman, 1976). However, weight loss in euphausiids preserved for up to one year would likely be less than 10% because of their large size and low lipid content (Sameoto, 1993[1]).

[1] D. Sameoto, Bedford Institute of Oceanography, Dartmouth, Nova Scotia B2Y 4A2, pers. commun. July 1993.

The higher mean stomach fullness indices during summer in the Bay of Fundy and winter on the Scotian Shelf indicate that these regions are seasonally important foraging areas for alewives. Off Nova Scotia, alewives fed most actively (judged by the proportion of feeding fish and their stomach fullness) where oceanic conditions, particularly depth (>200 m) and temperature, were suitable for *M. norvegica* (Kulka et al., 1982; Sameoto et al., 1993). Alewives prefer bottom temperatures of 7–11°C offshore at mid-depths in spring (101–183 m), in shallower nearshore waters in summer (46–82 m) and in deeper offshore waters in fall (119–192 m) (Stone and Jessop, 1992). During winter, *Meganyctiphanes* seeks deeper, warmer water rather than the cold upper layers (Bigelow, 1926; Hollingshead and Corey, 1974). While the seasonal pattern of movement by alewives (inshore and northward during spring and offshore and southward during fall) is partially linked with spawning migrations, it is apparent that their marine distribution is also influenced by the distribution, availability, and abundance of their main prey, *M. norvegica*.

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Literature cited

Ackman, R. G., C. A. Eaton, J. C. Sipos, S. N. Hooper, and J. D. Castell.
1970. Lipids and fatty acids of two species of North Atlantic krill (*Meganyctiphanes norvegica* and *Thysanoessa inermis*) and their role in the aquatic food web. J. Fish. Res. Board Can. 27:513–533.

Berkes, F.
1976. Ecology of euphausiids in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33:1894–1905.

Bigelow, H. G.
1926. Plankton of the offshore waters of the Gulf of Maine. Bull. U.S. Bur. Fish. 40:1–509.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. Bull. U.S. Fish Wildl. Serv. 74, 577 p.

Bowman, R. E.
1986. Effect of regurgitation on stomach content data of marine fishes. Env. Biol. Fish. 16:171–181.

Brett, J. R., and T. D. D. Groves.
1979. Physiological energetics. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (eds.), Fish physiology, Vol. 8, p. 280–344. Academic Press, New York.

Brooks, J. L.
1968. The effects of prey-size selection by lake planktivores. Syst. Zool. 17:272–291.

Brooks, J. L., and S. I. Dodson.
1965. The effect of a marine planktivore on lake plankton illustrates theory of size, competition and predation. Science 150:28–35.

Corey, S.
1988. Quantitative distributional patterns and aspects of the biology of the Mysidacea (Crustacea: Peracarida) in the zooplankton of the Bay of Fundy region. Can. J. Zool. 66:1545–1552.

Daan, N.
1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Neth. J. Sea Res. 6:479–517.

Durbin, A. G.
1979. Food selection by plankton feeding fishes. *In* H. Clepper (ed.), Predator-prey systems in fisheries management, p. 203–218. Sport Fishing Inst., Washington D.C.

Durbin, E. G., A. G. Durbin, R. W. Langton, and R. E. Bowman.
1983. Stomach contents of silver hake, *Merluccius bilinnearis*, and Atlantic cod, *Gadus morhua*, and estimation of their daily rations. Fish. Bull. 81:437–454.

Edwards, R. L., and R. E. Bowman.
1979. Food consumed by continental shelf fishes. 87–409 *In* H. Clepper (ed.), Predator-prey systems in fisheries management, p. 387–409. Sport Fishing Inst., Washington D.C.

Eggers, D. M.
1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34:290–294.

Elliott, J. M.
1972. Rates of gastric evacuation in brown trout, *Salmo trutta* L. Freshwater Biol. 2:1–18.

Elliott, J. M., and L. Persson.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977–991.

Evans, F.
1968. Development and reproduction of *Parathemisto gracilipes* (Norman) (Amphipoda, Hyperiidea) in the North Sea. Crustaceana 15:101–109.

Fange, R., and D. Grove.
1979. Digestion. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (eds.), Fish physiol., Vol. 8, p. 162–241. Academic Press, New York.

Fritz, E. S.
1974. Total diet comparison in fishes by Spearman rank correlation coefficients. Copeia 1974: 210–214.

Gilmurray, M. C.
1980. Occurrence and feeding habits of some juvenile fish in the southern bight of Minas Basin, Nova Scotia, 1979. Master's thesis, Acadia Univ., Wolfville, Nova Scotia, 100 p.

Gregory, R. S., G. S. Brown, and G. R. Daborn.
1983. Food habits of young anadromous alewives (*Alosa pseudoharengus*) in Lake Ainslie, Nova Scotia. Can. Field Nat. 97:423–426.

Herman, A. W., D. D. Sameoto, C. Shunnian, W. R. Mitchell, B. Petrie, and N. Cochrane.
1991. Sources of zooplankton on the Nova Scotia Shelf and their aggregations within deep shelf basins. Cont. Shelf Res. 11:211–238.

Holland, B. J., and G. F. Yelverton.
1973. Distribution and biological studies of anadromous fishes offshore North Carolina. N.C. Dep. Nat. Res. Spec. Sci. Rep. No. 24, 32 p.

Hollingshead, K. W., and S. Corey.
1974. Aspects of the life history of *Meganyctiphanes norvegica* (M. Sars), Crustacea (Euphausiacea), in Passamaquoddy Bay. Can. J. Zool. 52:495–505.

Huebner, J. D., and R. W. Langton.
1982. Rate of gastric evacuation for winter flounder, *Pseudopleuronectes americanus*. Can. J. Fish. Aquat. Sci. 39:356–360.

James, A. G.
1988. Are clupeid macrophagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. S. Afr. J. Mar. Sci. 7:161–177.

Janssen, J.
1976. Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*). J. Fish. Res. Board Can. 33:1972–1975.
1978a. Feeding-behaviour repertoire of the alewife, *Alosa pseudoharengus*, and the ciscoes, *Coregonus hoyi* and *C. artedii*. J. Fish. Res. Board Can. 35:249–253.
1978b. Will alewives (*Alosa pseudoharengus*) feed in the dark? Env. Biol. Fish. 3:239–240.

Janssen, J., and S. B. Brandt.
1978. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Can. J. Fish. Aquat. Sci. 37:177–184.

Jessop, B. M.
1990. Diel variation in density, length composition, and feeding activity of juvenile alewife, *Alosa pseudoharengus* Wilson, and blueback herring, *A. aestivalis* Mitchell, at near-surface depths in a hydroelectric dam impoundment. J. Fish Biol. 37:813–822.

Kulka, D. W., S. Corey, and T. D. Isles.
1982. Community structure and biomass of euphausiids in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 39:326–334.

Leim, A. H., and and W. B. Scott.
1966. Fishes of the Atlantic coast of Canada. Fish. Res. Board Can. Bull. 155, 485 p.

Locke, A., and S. Corey.
1988. Taxonomic composition and distribution of Euphausiacea and Decapoda (Crustacea) in the neuston of the Bay of Fundy, Canada. J. Plankton Res. 10:185–198.

Mauchline, J.
1984. Euphausiid, stomatopod and leptostracan crustaceans. E. J. Brill and W. Backhuys, London, 91 p.

Mauchline, J., and L. R. Fisher.
1969. The biology of euphausiids. *In* F. S. Russel and M. Yonge (eds.), Advances in marine biology, Volume 7. Academic Press, London, 454 p.

McLaren, I. A., M. J. Tremblay, C. J. Corkett, and J. C. Roff.
1989. Copepod production on the Scotian Shelf based on life-history analyses and laboratory rearings. Can. J. Fish. Aquat. Sci. 46:560–583.

Neves, R. J.
1981. Offshore distribution of alewife, *Alosa pseudoharengus* and blueback herring, *A. aestivalis*, along the Atlantic coast. Fish. Bull. 79:473–485.

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson.
1971. Food habits of albacore, bluefin tuna and bonito in California waters. Calif. Fish and Game Fish. Bull. 152:1–105.

Sameoto, D. D.
1982. Zooplankton and micronekton abundance in accoustic scattering layers on the Nova Scotian slope. Can. J. Fish. Aquat. Sci. 39:760–777.

Sameoto, D. D., L. O. Jaroszynski, and W. B. Fraser.
1980. BIONESS, a new design in multiple net zooplankton samplers. Can. J. Fish. Aquat. Sci. 37:722–724.

Sameoto, D., N. Cochrane, and A. Herman.
1993. Convergence of accoustic, optical,and net-catch estimates of euphausiid abundance: use of artificial light to reduce net-avoidance. Can. J. Fish. Aquat. Sci. 50:334–346.

Scott, J. S.
1972. Eggs and larvae of northern sand lance (*Ammodytes dubius*) from the Scotian Shelf. J. Fish. Res. Board Can. 29:1667–1671.

Sherman, K., and E. G. Schaner.
1968. Observations on the distribution and breeding of *Sagitta elegans* (Chaetognatha) in coastal waters of the Gulf of Maine. Limnol. Oceanogr. 13:618–625.

Siegel, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., Toronto, 312 p.

Sokal, R. R., and F. J. Rohlf.
1981. Biometry, 2nd ed. H. Freeman, San Francisco, 859 p.

Steedman, H. F.
1976. General and applied data on formaldehyde fixation and preservation of marine zooplankton. *In* H. F. Steedman (ed.), Zooplankton fixation and preservation, p. 103–154. Unesco Press, Paris, 350 p.

Stone, H. H.
1985. Composition, morphometric characteristics and feeding ecology of alewives (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*) (Pisces: Clupeidae) in Minas Basin. Master's thesis, Acadia Univ., Wolfville Nova Scotia, 191 p.

Stone, H. H., and G. R. Daborn.
1987. Diet of alewives, *Alosa pseudoharengus* and blueback herring, *A. aestivalis* (Pisces: Clupeidae) in Minas Basin, Nova Scotia, a turbid macrotidal estuary. Env. Biol. Fish. 19:55–67.

Stone, H. H., and B. M. Jessop.
1992. Seasonal distribution of river herring *Alosa pseudoharengus* and *A. aestivalis* off the Atlantic coast of Nova Scotia. Fish. Bull. 90:376–389.

Swynnerton, G. H., and E. B. Worthington.
1940. Notes on the food of fish in Haweswater (Westmoorland). J. Anim. Ecol. 9:183–187.

Vigerstad, T. J., and J. S. Cobb.
1978. Effects of predation by sea-run juvenile alewives (*Alosa pseudoharengus*) on the zooplankton community at Hamilton Reservoir, Rhode Island. Estuaries 1:36–45.

Vinogradov, V. I.
1984. Food of silver hake, red hake and other fishes on Georges Bank and adjacent waters, 1968–74. NAFO Sci. Counc. Studies 7:87–94.

Warshaw, S. J.
1972. Effects of alewives (*Alosa pseudoharengus*) on the zooplankton of Lake Warskopmic, Connecticut. Limnol. Oceanogr. 17:816–825.

Wells, L.
1970. The effects of alewife predation on zooplankton in Lake Michigan. Limnol. Oceanogr. 15:556–565.

Windell, J. T.
1978. Digestion and the daily ration of fishes. *In* T. Bagenal (ed.), Fish production in fresh waters, p. 227–254. Blackwell Scientific Publs., London, 365 p.

Queen conch, *Strombus gigas*, reproductive stocks in the central Bahamas: distribution and probable sources

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Abstract.—A survey of queen conch (*Strombus gigas*) populations near Lee Stocking Island, Exuma Cays, Bahamas, showed that 74% of all adults were on the narrow island shelf adjacent to the Exuma Sound, in 10–18 m of water. None were found deeper than 25 m, and relatively few adults were found shallower than 10 m. Numbers of juveniles were greatest on the Great Bahama Bank and decreased with increasing depth on the island shelf. No juveniles were found in shelf regions greater than 15 m in depth. Patterns of shell morphology, which were related to growth rates in juveniles, suggest that adults that mature on the Great Bahama Bank rarely move to deep water, and that the most important sources for deep-water stocks are small, nearshore nurseries on the island shelf. The mostly unfished deep-water populations are probably now the primary source of larvae for queen conch in the Exuma Cays. Because virtually all of the conch are within the limits of SCUBA diving, it will be important to identify and to protect critical nursery habitats for reproductive stocks.

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Queen conch (*Strombus gigas*), once abundant throughout the Caribbean region, have been fished to near extinction or to a level at which there is no longer a viable fishery in many localities (Appeldoorn et al., 1987; Berg and Olsen, 1989). This is particularly true in nations where the fishery has been open to SCUBA divers. Stock depletion resulted in at least temporary closures of the conch fishery in Bermuda, Florida, Cuba, Bonaire, and the U.S. Virgin Islands. Regulations including size limits, catch quotas, gear restrictions, and closed areas have been instituted in other countries.

This study was conducted in an attempt to understand reasons for the rapid depletion of queen conch populations in the Caribbean region, and to evaluate the significance of deep-water conch stocks. Several authors have suggested that these deep-water conch, living beyond the normal range of free divers, are the primary source of larvae for shall-water populations and the fishery (Berg and Olsen, 1989; Wicklund et al., 1991; Stoner et al., 1992; Stoner and Sandt, 1992). Therefore, we surveyed the density and age structure of queen conch in the vicinity of Lee Stocking Island in the central Bahamas. Differences in shell morphology and growth rate between conch found on Great Bahama Bank and on the windward island shelf adjacent to Exuma Sound were used as indicators of geographic source for reproductive stocks. The importance of deep-water populations is discussed in terms of fisheries management.

Methods and materials

Study site

An assessment of the adult conch population was conducted between 1989 and 1991 in a 12-km long section of the Exuma Cays, central Bahamas, adjacent to Lee Stocking Island (Fig. 1). To the west and south of the Cays lies the Great Bahama Bank, a shallow, sand- and seagrass-covered platform that extends to the Tongue of the Ocean. To the east and north is a narrow (1–2 km) island shelf, a steep shelf-break beginning at an approximately 30-m depth, and the deep Exuma Sound.

Great Bahama Bank in the region of the study site is characterized by strong tidal currents that carry oceanic water from Exuma Sound onto the bank through channels between the islands. Approximately 90% of the bank area is less than 3.5 m deep; the remainder is tidal channels with depths to 8 m near the inlets and between the Brigantine Cays. For this study the

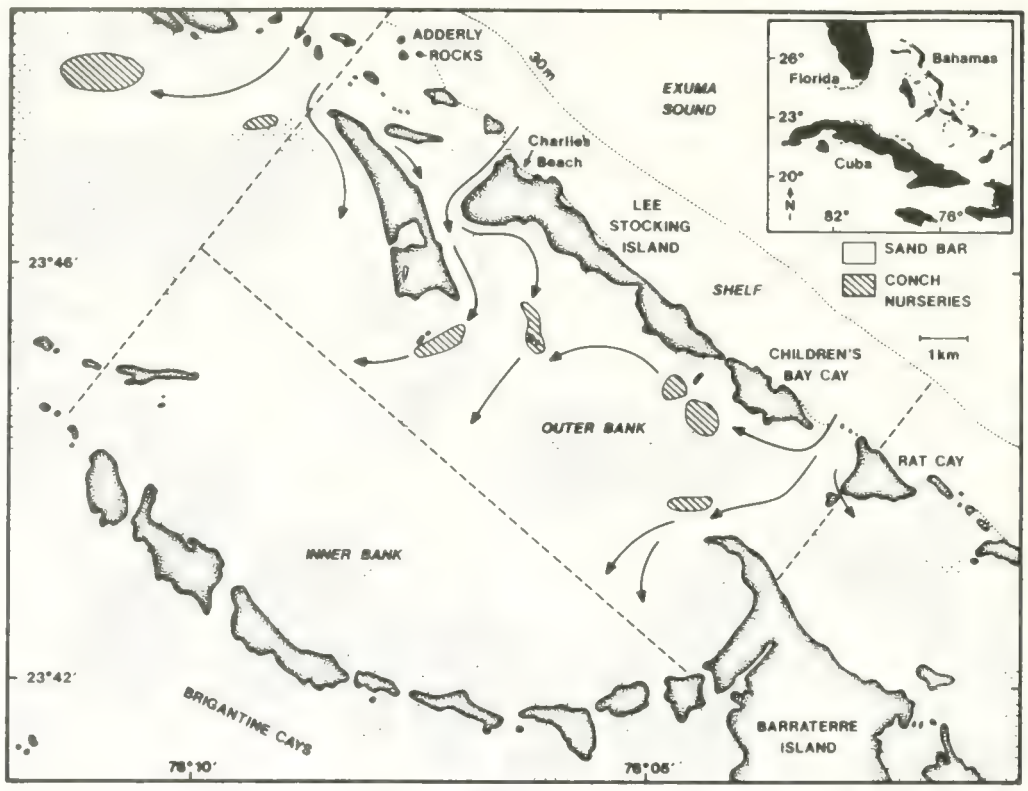

Figure 1

Map of the survey area near Lee Stocking Island, Exuma Cays, Bahamas. Flood tidal currents (arrows) and the locations of queen conch, *Strombus gigas*, nursery habitats (cross-hatched) are shown. Dashed lines separate the inner and outer bank regions and delineate the study site. Areas south and west of the Brigantine Cays were not surveyed.

bank was divided into an inner section from the Brigantine Cays to a line mid-way between the Brigantines and Lee Stocking Island, and an outer section from the mid-line to the cays at the eastern side of the bank (Fig. 1). Each section is approximately 5 km wide. The rationale for this division was that the outer section of the bank is flushed with oceanic water on every tide, while the inner bank is flushed only on extreme tides. Virtually all queen conch nurseries in the Exuma Cays are found within the outer 5.0 km of the bank (Stoner et al., in press.) (Fig. 1).

The eastern shores of the Exuma Cays are characterized primarily by steep aeolianite cliffs and beach rock interspersed with a few high-energy sandy beaches in coves, particularly on Lee Stocking Island and Children's Bay Cay. The seagrass *Thalassia testudinum* is found on shallow, soft-sediment platforms extending a short distance off the sandy beaches. Most of the shallow nearshore, however, is hard-bottom covered with a short turf of the green alga *Cladophoropsis* sp. The hard-bottom habitat, interspersed with small patches of sand and hard corals, is characteristic to 10-m depth. From 10 to 20 m the bottom comprises mixed hard-bottom and bare sand. Off Lee Stocking Island, corals form a 2-km long steep ledge from 10 to about 18 m, but a gradual slope to 25 m is typical of most of the study area. Patchy sand, coral, and hard-bottom are found between 20 and 30 m.

Detailed hydrographic charts are not available for the Exuma Cays; therefore, shelf bathymetry was mapped with 540 electronic depth-sounder points, corrected for tidal state, and positions acquired with Global Positioning System (GPS) from the RV *Challenger* during summer 1991. GPS positions taken at close intervals along the eastern shores of the islands were used as zero-depth data points. Three-dimensional plotting features of Systat 5.0 software were used to provide a bathymetric chart for the shelf region with 0, 2.5, 5, 10, 15, 20, 25 and 30 m contours for depth at mean low tide. Total surface area for each of the seven depth intervals was calculated with a digitizing board and SigmaScan 3.9 software. The surface area of the inner and outer bank regions was determined in a similar way with the aid of topographic maps.

Survey methods

The shelf region was surveyed in each of seven depth zones between 2.5 and 30 m (described above) along nine transects (perpendicular from the Cays into Exuma Sound) placed at approximately 1.0-km intervals. At each of the 63 shelf stations, divers swam parallel to the isobaths for a distance measured with a calibrated General Oceanics flow meter equipped with a large propeller for low velocity flows. Calibration was performed by towing the meter repeatedly ($n \geq 6$) through calm water at the side of a small boat over a pre-measured distance of 100 m. Precision was ±2%. Current velocity on the shelf adjacent to Lee Stocking Island is generally low (<3 cm/sec) and to the northwest, parallel to the isobaths (Smith, 1992[1]). Recognizing the potential effect of current on the calculated distance, each dive included two legs, one up-current and one down-current in parallel lines of equal length separated by approximately 20 m.

Two dives were made at most stations for density determinations and shell measurements (described below). For density, all queen conch were counted in an 8-m wide path defined by a line held between two divers. The average swim distance was 380 m, resulting in coverage of just over 3000 m^2. Conch density was calculated by using only those conch in the 8-m band. Shell measurements were made for animals outside the 8-m band in areas with low conch densities. Underwater visibility was usually high and the area of bottom searched was actually much larger than the swim path alone. Consequently, all conch within approximately 30 m could be collected for measurement. In areas where conch densities were high, one dive was made to collect density data and another to collect only measurement data. An attempt was made to measure at least 100 adults from each depth zone, but this was not possible in the 0–5, 5–10, and 25–30 m zones because of low densities in these zones. Statistical differences in density among the survey zones were evaluated with the non-parametric Kruskal-Wallis test (Sokal and Rohlf, 1969) with stations used as replicates (n=9).

The shallowest depth zone (0–2.5 m) was limited primarily to sandy coves on the major islands of the survey area. Adult queen conch were few in these areas, and juveniles were distributed unevenly; therefore, the important seagrass areas of the shallow coves were thoroughly searched. Density measures were not made but all conch encountered were measured (as described below).

[1] N. P. Smith, Harbor Branch Oceanography Inst., Fort Pierce, FL, pers. commun. 1992.

Sparse distribution of adult conch and the large surface area of the Great Bahama Bank required the use of different survey methods from those applied on the shelf. Because the bank waters are shallow and conch were easily seen, large areas were surveyed by towing a diver at the surface in continuous lines. The bank region was divided into 95 — 1 × 1 km squares oriented along lines of latitude. Then, in a systematic grid of lines running diagonally through the squares, every square was crossed at least once during the survey. Additional tows were made in areas already known to have concentrations of adults, i.e., near nurseries previously mapped (Fig. 1; Stoner et al., in press.). Divers were towed a total distance of 126 km.

Although water clarity on the bank was not as high as that on the island shelf, the towed diver could usually see at least 2.5 m on either side of the transect line. Surveys were not conducted on a few days when visibility was restricted. While being towed at approximately 50 cm/sec, the diver signaled numbers of adult queen conch to the boat operator, who recorded position. Positions for the ends of all straight line transects were determined with GPS, tow distance was estimated by chart, and conch density was calculated on the basis of the 5-m wide path examined. During the bank survey, 472 adults were gathered and measured. Presence of juveniles on the bank was noted but not quantified in this study. For comparison with shelf sites, a random collection of 322 juvenile conch was made from a nursery west of Lee Stocking Island during August 1991. These conch were measured for shell length.

The total number of adult queen conch was estimated crudely for each bank and shelf area by extrapolating the average density of conch for an individual zone over the total surface area for the same zone. Because variances in the density data were large, confidence intervals for the extrapolated numbers of conch were not calculated.

Shell measurements

Queen conch reach sexual maturity between 3.5 and 4 years of age, a few months after the shell edge has formed a broadly flared lip (Appeldoorn, 1988). After the lip flares, queen conch stop growing in length but continue to deposit shell material on the inside of the lip (Egan, 1985; Appeldoorn, 1988). Therefore, with certain limitations, thickness of the shell lip is an indicator of approximate age (Stoner and Sandt, 1992). In this study, shell-lip thickness was measured with calipers in the area of greatest thickness, about two-thirds of the distance posterior from the

siphonal groove and 35 mm in from the edge of the shell, according to the methods of Appeldoorn (1988) and Stoner and Sandt (1992). Shell length was measured from the tip of the spire to the end of the siphonal canal in both adults and juveniles. Repeated measures made by different persons showed that both length and lip thickness measurements were made to ±1 mm. Differences in length-frequency and thickness-frequency distributions were tested with the non-parametric Kolmogorov-Smirnov test.

Morphological differences between bank and shelf populations were tested with canonical discriminant function analysis from shell length and lip thickness data. This multivariate technique is well suited for differentiating two types where individual characteristics do not separate the types. The analysis computes a third variable Z, which is a linear function of both variables (length and thickness, in this case) such that the equation for the new line maximizes the distance between the two types (Sokal and Rohlf, 1969). The significance of the discriminant function Z was determined with the Hotelling-Lawley trace test statistic (Morrison, 1976). Results of the canonical analysis were then examined to determine what percentage of the individuals were correctly classified according to collection site.

Observations were also made on general shell thickness (particularly in juveniles), length of apical spines and resultant shell diameter, and number of spines per whorl. None of these characteristics were quantified systematically.

Shell growth experiment

Early observations suggested that shell phenotypes were different between shelf and bank conch. Adults from the shelf appeared to be longer and to have thicker shell lips than those from the bank. Juveniles from the shelf were more narrow, thin-lipped, and had shorter apical spines than those on the bank (Martin-Mora, 1992). To examine the potential relation between shell morphology and growth rates, juveniles were tagged in two different nursery sites: in the well-studied nursery west of Children's Bay Cay and in seagrass areas off Charlie's Beach in the northeast cove of Lee Stocking Island (Fig. 1). Juveniles were individually marked with spaghetti tags (Floy Tag & Manufacturing Co.) tied around the spire and measured to the nearest millimeter with calipers. Charlie's Beach conch between 108 and 150 mm (mean=137 mm, n=281) were measured and released in the last week of August 1990. Children's Bay Cay conch, somewhat smaller than the Charlie's Beach conch (106 to 133 mm, mean=118 mm, n=292), were tagged and released in early September 1990. Conch from both populations were remeasured for shell length five months later, at the end of February 1991. Forty-eight conch were recovered at Charlie's Beach and 135 were recovered at the Children's Bay Cay site. Daily growth rate was calculated for individuals by dividing increase in length by the number of days between measurements. Differences in growth rate between the two sites were evaluated by using the Mann-Whitney U-test.

Results

Conch densities and abundance

Densities of adult queen conch in the survey area were highest between 15 and 20 m depth on the island shelf (Table 1) with nearly 88 conch/ha (Fig. 2). Density was also high between the 10– and 15-m isobaths. In both of these depth zones densities of adults were highly variable, but there was no apparent pattern across transect lines. There was a highly significant difference in the density of adult conch in the survey zones (Kruskal-Wallis test, $H_{adj.}$=36.195, P<0.001)(Fig. 2). No conch were found deeper than 25 m, despite an abundance of apparently suitable habitat of sand and algae-covered hard-bottom. Adults were most sparsely distributed

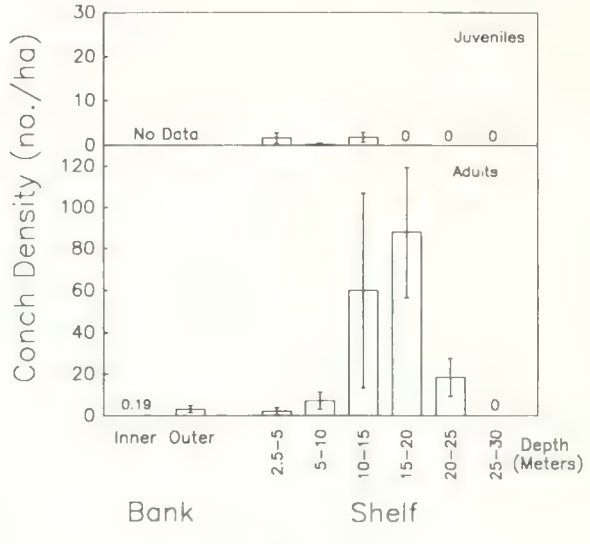

Figure 2

Density of queen conch, *Strombus gigas*, on the Great Bahama Bank and in six different depth zones of the island shelf hear Lee Stocking Island, Bahamas. Values are ± mean standard error of the mean.

Table 1

Estimated total number of adult queen conch, *Strombus gigas*, in a 12-km section of the Exuma Cays, Bahamas, between Adderly Rocks and Rat Cay.

Region	Total area (ha)	Density (no./ha) (mean ± SE of mean)	Total no. of conch
Bank			
Inner	4,979	0.19 ± 0.14	946
Outer	3,997	3.16 ± 1.69	12,631
Bank total	8,976		13,577
Shelf			
0–2.5 m	161	Low — not qualified	Negligible
2.5–5 m	198	2.24 ± 1.70	444
5–10 m	465	7.21 ± 4.11	3,353
10–15 m	429	60.1 ± 46.8	25,800
15–20 m	454	87.9 ± 31.5	39,902
20–25 m	320	18.3 ± 9.1	5,843
25–30 m	151	0 ± 0	0
Shelf total	3,687		75,342
Grand Total	12,663		88,919

in the inner section of the Great Bahama Bank with only 0.19 conch/ha (SD=0.15, n=28). Density of adult conch in the outer (seaward) section of the bank was close to the value for the 2.5–5 m depth zone on the shelf. Although not quantified, numbers of adults in the nearshore (0–2.5 m) zone of the shelf were negligible.

Few juvenile conch were observed on the shelf between 2.5-and 15-m depth (Fig. 2). A total of 372 juveniles were found in densely aggregated patches on seagrass beds off the eastern beaches of Lee Stocking Island. On the Great Bahama Bank, most juveniles were aggregated in specific nursery locations documented previously (Stoner et al., in press.). None was found deeper than 15 m.

The area between 10 and 20 m depth on the island shelf was a particularly important habitat for adult queen conch (Table 1). Approximately 74% of all conch in the 12-km long survey area reside in this narrow depth zone. It is also clear that large expanses of shallow bank habitat support a relatively small proportion (15.2%) of the adult population. Mating conch and demersal egg masses were very abundant during summer months at shelf sites deeper than 10 m, but none were observed on the bank.

Shell morphology

The shelf sites were characterized by large adult queen conch, primarily between 200 and 260 mm (mean=227, SD=23, n=572), whereas most adult conch on Great Bahama Bank were between 170 and 210 mm shell length (mean=187, SD=16, n=472). Pooling all adults measured, there was a highly significant difference in the length-frequency distribution of conch on the shelf and on the bank (Kolmogorov-Smirnov test, P<0.001). The distributions (Fig. 3) show clearly the separation in size of adults between bank and shelf sites, particularly when comparing nearshore (0–5 m) shelf zones with those from the bank. The distributions show a decrease in shell length between the nearshore shelf and deeper zones, while those between 5 and 25 m are obviously similar.

Bank conch had thin shell lips (mean=10, SD=6); conch from nearshore (2.5–5 m) regions of the shelf were intermediate in lip thickness (mean=18, SD=5); and deep-shelf (5–25 m) conch had the thickest shell lips (mean=30, SD=7)(Fig. 4). All three of these groups were significantly different from one another in terms of lip thickness distribution (Kolmogorov-Smirnov tests, P<0.01). There was obvious similarity in the thickness distributions of shells in depth zones between 5 and 25 m; therefore, these four depth categories were pooled.

Distinctness of the morphs collected on the bank and shelf is further suggested by a plot of shell length and lip thickness for 250 randomly chosen individuals from each of the two regions (Fig. 5). Also, when length and lip thickness data for all 1,029 conch measured in the survey were used in canonical discriminant function analysis, a highly significant separation was found between conch collected in the two different regions (Hotelling-Lawley Trace, F=1,854, P<0.001). Less than 5% of the conch in the survey were not collected in the region predicted by the multivariate equation. Bank conch were small and had thin shell lips, whereas conch from the island shelf were large and had thick shell lips. Results of the analysis, however, do not rule out the possibility that the smallest adult conch from the shelf region, particularly apparent in the 5–10 m depth zone, could be older animals from the bank.

Length-frequency distributions of juvenile queen conch were different on the Great Bahama Bank and island shelf (Fig. 6). Both the bank and nearshore

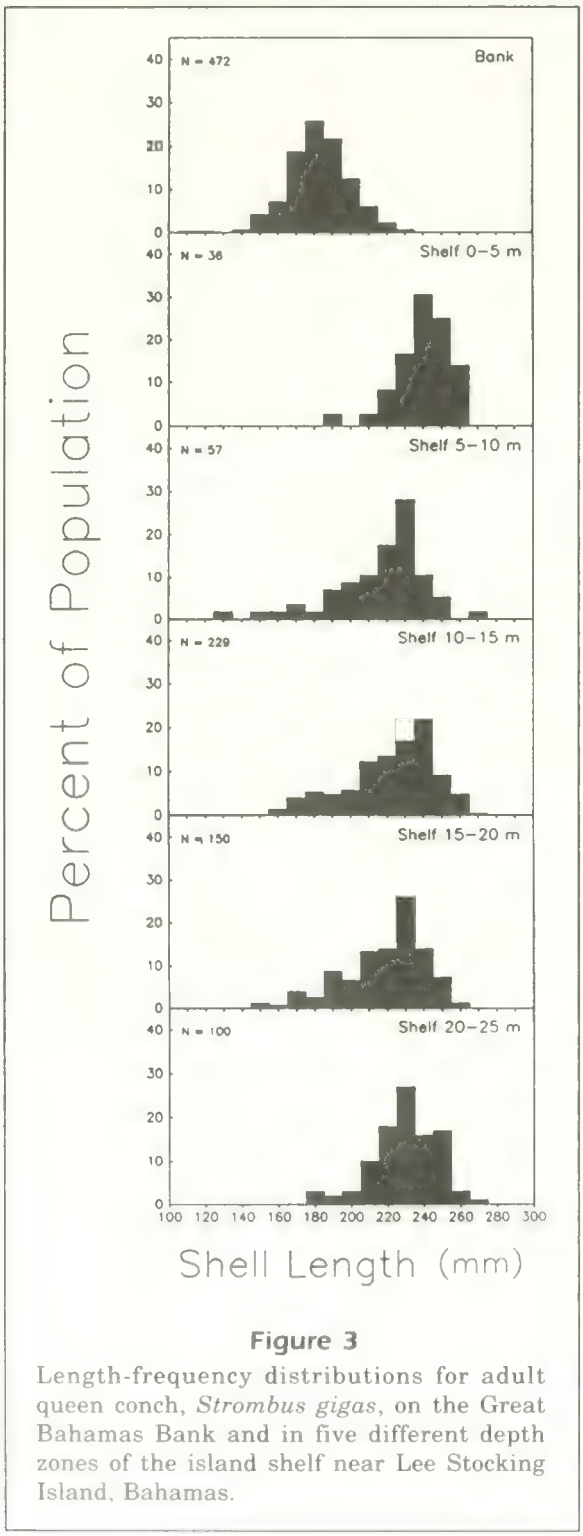

Figure 3

Length-frequency distributions for adult queen conch, *Strombus gigas*, on the Great Bahamas Bank and in five different depth zones of the island shelf near Lee Stocking Island, Bahamas.

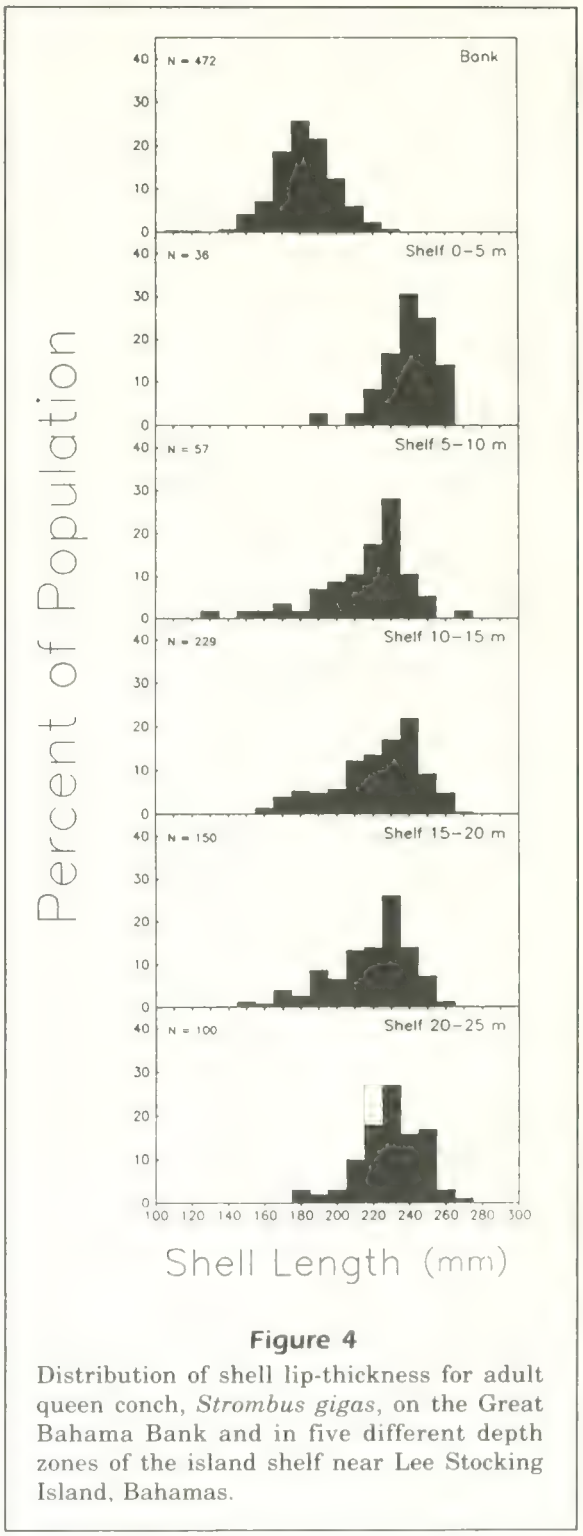

Figure 4

Distribution of shell lip-thickness for adult queen conch, *Strombus gigas*, on the Great Bahama Bank and in five different depth zones of the island shelf near Lee Stocking Island, Bahamas.

(0–2.5 m) shelf had juveniles less than 100 mm in shell length; however, these were rare in the shelf environment, and few juveniles less than 160 mm were found on the shelf between 2.5- and 15-m depth. None of the juveniles on the bank were near the 227-mm average length of adults on the shelf, but many juveniles collected in deeper water were close to adult size.

Other differences were observed in the shells of queen conch from bank and shelf regions. Juvenile conch from the bank differed from shelf juveniles because of thicker shells and longer lateral spines

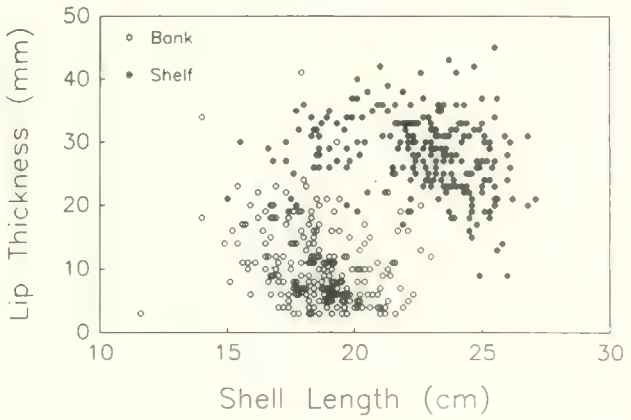

Figure 5

Scatterplot of shell lip-thickness vs. shell length for adult queen conch, *Strombus gigas*, collected from the Great Bahama Bank and from the Lee Stocking Island shelf. Two-hundred and fifty randomly chosen points were plotted for each site.

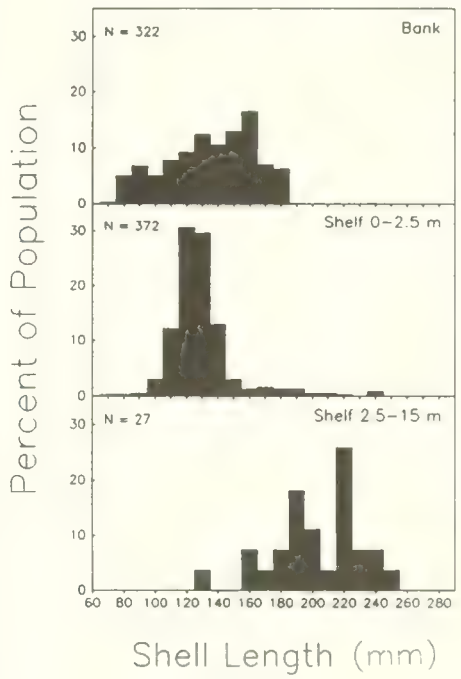

Figure 6

Length-frequency distribution for juvenile queen conch, *Strombus gigas*, from the Great Bahama Bank and from two depth zones on the island shelf near Lee Stocking Island, Bahamas.

(5–6 spines/whorl vs. 7–9 spines/whorl in shelf juveniles). Bank conch had a maximum shell diameter between 80 and 90% of shell length at 100 mm length, whereas juveniles from the shelf had diameters between 50 and 60% of shell length. These characteristics persisted to adult stages with bank conch having longer spines. The outer whorls of shelf adults, even young individuals, were often nearly smooth.

Growth rates

Juvenile queen conch on the island shelf at Charlie's Beach grew in length at a rate approximately 2.4 times the rate observed at the Children's Bay Cay site. Conch recovered at Charlie's Beach grew 0.139 mm/day (SD=0.025, n=135). At Children's Bay Cay, mean growth rate was 0.058 mm/day (SD=0.021, n=48). The differences in growth rate between bank and shelf juveniles were highly significant (Mann-Whitney U-test, $P<0.001$).

Discussion

The rapid increase in adult queen conch density at depths greater than 10 m is probably a direct function of fishing, which is limited to free-diving on the bank and shallow nearshore shelf areas around Lee Stocking Island. This conclusion is substantiated by observations of conch depth distribution in other localities. In unfished areas of Islas Los Roques, Venezuela, Weil and Laughlin (1984) found that density of queen conch was highest in 4.0 m of water and density decreased with depth to 18 m. This may represent the natural distribution of queen conch. In comparable 4-m deep habitats not protected from fishing, densities were 5 times less than those in the protected area. Similarly, in the Exuma Land and Sea Park, a 500-km^2 fishery reserve 90 km north of Lee Stocking Island, there are large numbers (unquantified) of adult conch at 2–4 m depth, and many of these shallow-water conch have been observed laying eggs (Stoner, pers. observ.); whereas adults are uncommon in shallow water near Lee Stocking Island and spawning has never been observed at less than 5 m depth. Similar to the pattern reported in this study for Lee Stocking Island, Torres-Rosado (1987) found maximum density of adult queen conch between 10 and 20 m in Puerto Rico, where fishing is heavy in shallower waters.

It is recognized that queen conch move to greater depths with age and size (Randall, 1964; Weil and Laughlin, 1984); this has been confirmed in the Lee Stocking Island area by the recovery of individuals that were tagged as juveniles at Charlie's Beach and subsequently found in deeper offshore waters

(Stoner, unpubl. data). However, our morphological analyses of conch suggest that very few conch using the bank for a nursery actually reach the offshore spawning sites. Furthermore, similarities in length frequency and shell morphology between juveniles found immediately off the east (windward) side of the Cays on isolated seagrass beds and adults in deep water suggest that the small aggregations of juveniles found on the shelf serve as the primary source for the offshore reproductive stocks. Given that mating and egg-laying are rare on the Great Bahama Bank, it is likely that recruitment to bank nurseries is sustained by deep-water reproductive populations (Wicklund et al., 1991; Stoner et al., 1992; Stoner and Sandt, 1992).

Differences in shell morphology between bank and shelf conch are not well understood but appear to be related to growth rate. Alcolado (1976) reported that large, thin shells and short spines in queen conch in Cuba were associated with rapid growth. A similar phenomenon may explain the shell differences observed in this study. Juveniles in the nearshore shelf environment of Charlies' Beach grew rapidly and had the large, thin-shelled, short-spined morphotype typical of the shelf adults. The small, thick-shelled, long-spined conch on the bank had growth rates less than half of those on the shelf. A recent transplant experiment at Lee Stocking Island demonstrated that shell form and spination in juvenile conch is an environmentally mediated characteristic associated with habitat type and individual growth rate (Martin-Mora, 1992).

The large size of the deep-water reproductive stock may explain high productivity of queen conch in the Exuma Cays. It is likely, however, that abundance of conch in the region is now dependent upon the small, isolated pockets of fast-growing juveniles that inhabit the nearshore shelf habitat during the first two or more years of life then recruit to deep-water reproductive populations. Stoner and Sandt (1992) found that the adult population at an 18-m deep site off Lee Stocking Island was relatively stable between 1988 and 1991, but most individuals were old and thick-lipped. The predominance of old conch in deep water may or may not be a function of low recruitment rates from shallow water in recent years, and the significance of shallow-water spawning to conch abundance is unknown.

In an comparison of data from Glazer and Berg (in press.), densities of queen conch in the Exuma Cays are 10 to 100 times higher than those reported for many other localities in the Caribbean region. This may be related to geographic differences in habitat quality, recruitment processes, and fishing methods. The Exuma Cays probably represent a particularly efficient system for retaining conch larvae because of unique geographic and oceanographic conditions such as an alongshore current and numerous tidal inlets leading to nursery grounds (Stoner et al., in press), but fishing methods can play a large role in the population structure of queen conch. Fishing in the Bahamas is restricted to free-diving and limited diving with surface-supply air for adults with flared shell lips; therefore, conch deeper than 10 m are rarely exploited. Depth distribution of queen conch near Lee Stocking Island suggests that virtually every conch in the Exuma Cays is within the range of SCUBA divers and that populations of *S. gigas* could be decimated quickly if the fishery were opened to this latter gear. On the other hand, if the source of deep-water conch is shallow-water nurseries, protection of deep-water reproductive stocks only delays the effects of overfishing, and certain nurseries should be protected as well. Analysis of larval transport and recruitment processes will be crucial to the sound management of this already threatened commercial species.

Acknowledgments

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Literature cited

Alcolado, P. M.
1976. Crecimiento, variaciones morfologicas de la concha y algunos datos biologicos del cobo *Strombus gigas* L. (Mollusca, Mesogastropoda). Acad. Ciencias de Cuba, Inst. de Oceanol. No. 34, 36 p.

Appeldoorn, R. S.
1988. Age determination, growth, mortality, and age of first reproduction in adult queen conch, *Strombus gigas* L., off Puerto Rico. Fish. Res. 6:363–378.

Appeldoorn, R. S., G. D. Dennis, and O. Monterrosa-Lopez.
1987. Review of shared demersal resources of Puerto Rico and the lesser Antilles region. *In* R. Mahon (ed.), Report and proceedings of the expert consul-

tation on shared fishery resources of the lesser Antilles region. FAO Fish. Rep. 383:36–106.

Berg Jr., C. J., and D. A. Olsen.
1989. Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. *In* J. F. Caddy (ed.), Marine invertebrate fisheries: their assessment and management. Wiley & Sons, NY, p. 421–442.

Egan, B. D.
1985. Aspects of the reproductive biology of *Strombus gigas*. M.S. thesis, Univ. British Columbia, Vancouver, Canada, 147 p.

Glazer, R. A., and C. J. Berg Jr.
In press. Current and future queen conch, *Strombus gigas*, research in Florida. *In* R. S. Appeldoorn and B. Rodriguez (eds.), The biology, fisheries, mariculture, and management of the queen conch. Fundacion Cientifica Los Roques, Caracas, Venezuela.

Martin-Mora, E.
1992. Developmental plasticity in the shell of the queen conch, *Strombus gigas*. M.S. thesis, Florida State Univ., Tallahassee, 52 p.

Morrison, D. F.
1976. Multivariate statistical methods. McGraw-Hill, New York.

Randall, J. E.
1964. Contributions to the biology of the queen conch, *Strombus gigas*. Bull. Mar. Sci. 14:246–295.

Sokal, R. R., and F. J. Rohlf.
1969. Biometry. W. H. Freeman, San Francisco, 776 p.

Stoner, A. W., and V. J. Sandt.
1992. Population structure, seasonal movements, and feeding of queen conch, *Strombus gigas*, in deep-water habitats of the Bahamas. Bull. Mar. Sci. 51:287–300.

Stoner, A. W., V. J. Sandt, and I. F. Boidron-Metairon.
1992. Seasonality in reproductive activity and larval abundance of the queen conch, *Strombus gigas*. Fish. Bull. 90:161–170.

Stoner, A. W., M. D. Hanisak, N. P. Smith, and R. A. Armstrong.
In press. Large-scale distribution of queen conch biology, fisheries, and mariculture: implications for stock enhancement. *In* R. S. Appeldoorn and B. Rodriguez (eds.), The biology, fisheries, mariculture, and management of the queen conch. Fundacion Cientifica Los Roques, Caracas, Venezuela.

Torres-Rosado, Z. A.
1987. Distribution of two mesogastropods, the queen conch, *Strombus gigas* Linnaeus, and the milk conch, *Strombus costatus* Gmelin, in La Parguera, Lajas, Puerto Rico. M.S. thesis, Univ. Puerto Rico, Mayaguez, 37 p.

Weil, E., and R. Laughlin.
1984. Biology, population dynamics, and reproduction of the queen conch, *Strombus gigas* Linne, in the Archipielago de Los Roques National Park. J. Shellfish Res. 4:45–62.

Wicklund, R. I., L. J. Hepp, and G. A. Wenz.
1991. Preliminary studies on the early life history of the queen conch, *Strombus gigas*, in the Exuma Cays, Bahamas. Proc. Gulf Caribb. Fish. Inst. 40:283–298.

Abstract.—Regression and time series analyses were used to investigate the relation between Apalachicola River flows and blue crab, *Callinectes sapidus*, harvests in and around Apalachicola Bay, Florida. Apalachicola River flows in one year were positively correlated with Franklin County blue crab landings during the next year (r^2=0.32, P<0.001, 1952-90), and the strength of the correlation increased when only more recent years were examined (r^2=0.49, P=0.001, 1973-90). In this area, blue crabs mature to a harvestable size by one year of age. Apalachicola River flows were also correlated with neighboring Wakulla County blue crab landings with a one-year time lag (r^2=0.52, P=0.001, n=17), but were not associated with blue crab landings for the remaining west coast of Florida. The mean monthly flow from September to May, termed the growout period, was the parameter most highly correlated with the following year's blue crab landings. Of five north Florida rivers examined, the Apalachicola River was most highly correlated with Franklin and Wakulla County blue crab landings.

Results of this study further document the influence of Apalachicola River flows on estuarine productivity. The positive relation between flows and blue crab harvests a year later suggests that low flow conditions in the estuary during the growout period negatively affect juveniles. Although the underlying causes of the correlations are not known, the effect of inflows on estuarine salinity is one of several possible mechanisms that warrants further investigation.

The influence of Apalachicola River flows on blue crab, *Callinectes sapidus*, in north Florida

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River flow affects many characteristics of estuaries, including salinity, turbidity, and nutrient and detrital concentrations. Changes in flow, therefore, may significantly affect estuarine biota, the extent to which may be inferred by examining historical relations between flow and productivity. Apalachicola Bay, Florida, like many estuaries, is subject to changes in freshwater inflow related to factors such as rainfall and upstream demands for agricultural, municipal, and industrial uses. Plans to reallocate freshwater resources (U.S. Army Corps of Engineers, 1989[1]) have renewed interest in the question of how freshwater inflows are related to productivity in the Apalachicola River and Bay system. This study examined the historical relationship between Apalachicola River flows and estuarine productivity.

One method of characterizing the importance of freshwater inflow to estuarine productivity is to correlate historical flow data with the commercial catch (landings) of estuarine-dependent species (Funicelli, 1984). Commercial landings are used to estimate estuarine productivity because they are often the only available long-term records from which species abundance can be inferred. Long-term records are available for several commercially important species in Apalachicola Bay, including oysters and blue crabs, which have different trophic requirements and estuarine residency patterns. By examining associations between these species and Apalachicola River flows, effects of freshwater delivery upon estuarine productivity can be evaluated. Associations between freshwater inflows and Apalachicola oyster harvests have been previously addressed (Wilber, 1992). The present study examines the influence of Apalachicola River flows on local and regional commercial blue crab, *Callinectes sapidus*, landings. Other north Florida rivers were also examined to estimate the relative importance of the Apalachicola River to blue crab landings with respect to these drainages.

Blue crabs in the Gulf of Mexico reach a harvestable size within a year of age (Perry, 1984) and comprise a significant portion of the commercial landings by 18–months of age (Steele, 1992[2]). Blue crabs enter the Apalachicola estuary as megalopae and young juveniles, reaching peak juvenile abundances in the winter (Livingston, 1983). Young crabs concentrate in the less saline portions of the bay, whereas egg-bearing females remain in the higher-salinity gulf waters where they spawn. It has been proposed that adult female blue crabs along the Florida gulf coast migrate to

[1] U.S. Army Corps of Engineers, Mobile District. 1989. Draft Post Authorization Change Notification Report for the Reallocation of Storage from Hydropower to Water Supply at Lake Lanier, Georgia, 320 p.

[2] P. Steele, Florida Marine Research Inst., 108th Ave. SE, St. Petersburg, FL 33701, pers. commun. 1992.

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gulf waters near Apalachicola Bay to spawn and that the larvae are distributed to the south by loop currents (Oesterling and Evink, 1977). Evidence supporting this hypothesis was examined in this study.

Methods

Fisheries data

Several aspects of the blue crab fishery may lead to inaccurate fishery representation of adult stock abundance. For example, unreported landings from the recreational fishery and crab bycatch from the shrimp fishery are potential sources of bias in blue crab landings statistics (Perry, 1984). Although these sources of error cannot be controlled, if they are independent of river flow and account for a relatively constant proportion of the total landings over time, a valid, although perhaps conservative, representation of environmental effects on the species can be obtained.

The Florida Department of Natural Resources (FDNR) provided monthly landing data for blue crabs from Franklin and Wakulla Counties for 1979–90, monthly effort data (number of trips) for 1987–90, annual landing data from Wakulla County from 1973 to 1990 (excluding 1977), and annual landing data from the Florida west coast from 1960–1990. Franklin County annual landing data from 1952 to 1979 were also obtained (Herbert et al., 1988[3]). Statistical analyses (Wilkinson, 1990) were conducted by using the full 39-year Franklin County dataset, as well as a shorter (1973–90) dataset, which allowed comparisons between Franklin and Wakulla Counties that were not confounded by differences in time periods. The limited amount of effort data precluded analyses of catch per unit of effort.

Flow and rainfall data

The Apalachicola River begins at the Florida state line by the confluence of the Chattahoochee and Flint Rivers. Apalachicola flow data were collected at the United States Geological Service gauge at Blountstown, Florida, which is the closest station to the estuary (105 km upstream) with an adequate period of record. This station is not immediately adjacent to the estuary, therefore fresh water from local inputs and storm events are not included. The drainage area downstream from the Blountstown gauge is less than 9% of the total area drained by the Apalachicola-Chattahoochee-Flint River system (Leitman et al., 1983[4]).

Parameters examined included the highest and lowest average flows for 7 and 120–consecutive days each year (referred to as the 7- and 120-day maximum and minimum flows). Monthly minimum, mean, and maximum values, and the mean monthly flow during the growout period (September–May) were also examined. By using these flow durations, associations between landings and seasonal high and low flows could be examined, which was not possible when analyses included only mean annual flow. The growout-flow time period was adapted from a similar study correlating blue crab landings in Georgia with river discharges (Rogers et al., 1990[5]).

Sufficient historical flow data were also available for the Suwannee, Econfina, St. Marks, and Ochlockonee Rivers (Fig. 1), thus permitting a regional analysis of associations between flows and blue crab landings. For each river, the annual one-day minimum, one-day maximum, and annual mean flows were used. One-day high and low flow magnitudes were used because of their availability and because preliminary analyses which substituted other flow durations (annual minimums and maximums) on the Apalachicola River did not change results considerably.

Statistical analyses

Blue crab landings and flow data were tested for monthly, seasonal, and inter-annual dependencies through autocorrelations. Data were adjusted to remove dependencies when autocorrelations were significant. If autocorrelations between successive months were present, data were replaced by the difference between each month and the preceding month. If seasonal autocorrelations were present, the effects were removed by dividing each value by a seasonal factor. For instance, if landings exhibited a significant autocorrelation with a 12-month time lag, which reflected a similarity in catches for the same month among years, each monthly value was divided by the month's mean value and replaced by the quotient. Similar analyses were conducted with seasonal (three-month averages) landings and flow data following adjustments to remove significant autocorrelations. Flow data were $\log_{10}$ transformed.

[3] Herbert, T. A., and Associates. 1988. The Franklin County Fisheries Options Report, 164 p.

[4] Leitman, H. M., J. E. Sohm, and M. A. Franklin. 1983. Wetland hydrology and tree distribution of the Apalachicola River flood plain, Florida. U.S. Geological Survey Water-Supply Paper 2196, 52 p.

[5] Rogers, S. G., J. D. Arrendondo, and S. N. Latham. 1990. Assessment of the effects of the environment on the Georgia blue crab stock. Final Rep. Georgia Dep. Natl. Resources, 69 p.

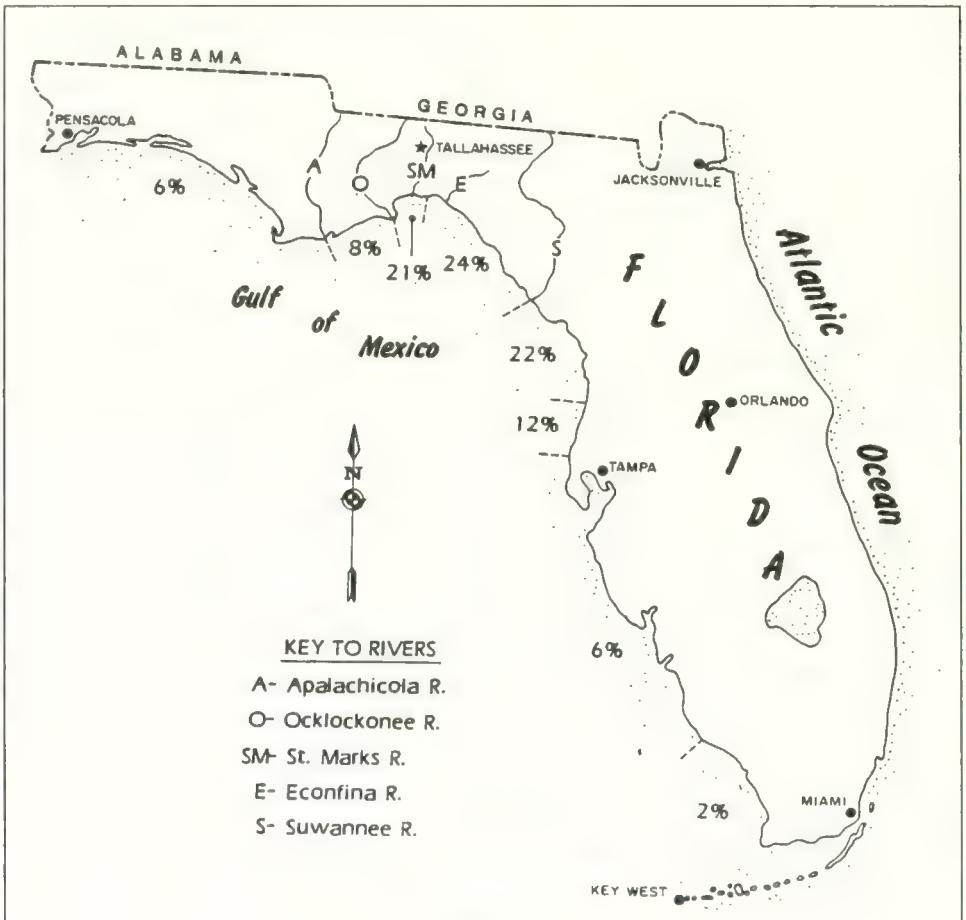

Figure 1

Percentage of total Florida west coast blue crab (*Callinectes sapidus*) landings caught by area (Steele, 1982). The five rivers used in the multivariate regression analyses (Apalachicola, Ochlockonee, St. Marks, Econfina, and Suwannee) are depicted.

Autoregressive order 1 (ARIMA) models were conducted on the Franklin and Wakulla County blue crab annual data and the residuals from these analyses were correlated with flow. This approach provided statistically rigorous estimates of *P*-values for the flow/landings relationships that were independent of any effects resulting from the one-year autocorrelations in landings. Analyses that used the ARIMA residuals and those that used unadjusted blue crab landings data were reported because both methods impart useful information. Correlations that used unadjusted annual blue crab data, i.e., significant autocorrelations were not removed, were biologically relevant because feedback mechanisms inherent to these autocorrelations (such as reproduction and recruitment) may also be associated with flow. Results of analyses that used unadjusted data are also more readily compared to results of other studies. Use of ARIMA models statistically validated the significant relations between blue crab landings and flow data, but may have removed some biologically relevant information. This paper primarily refers to unadjusted regression results.

Regression analyses incorporating a one-year time lag between flows and landings were conducted to examine the effects of flow on early blue crab life history stages. Contemporaneous analyses were conducted to assess the effect of flow on adults.

Univariate and stepwise multivariate regression analyses were conducted to estimate the amount of variability in blue crab landings accounted for by five major rivers on Florida's northern gulf coast. The criterion for admitting a flow variable into the stepwise regression models was an *F*-statistic greater than 4.0 for its partial correlation with landings. Data on blue crab landings for the west coast of Florida were used as a dependent variable in some analyses. To more specifically examine

whether there was evidence that the Apalachicola River affects blue crab landings on a regional basis, Franklin and Wakulla landings were removed from the west coast dataset. Regression analyses were conducted to test whether Apalachicola flows and the remaining west coast landings were significantly related.

Results

Annual landings

Blue crab landings varied nearly 10-fold over the period of record examined in each county (Fig. 2). Significant autocorrelations between consecutive years were present in both Franklin (r^2=0.19, P=0.006) and Wakulla (r^2=0.37, P=0.016) County landings. Annual flow parameters did not exhibit any significant autocorrelations.

Annual Franklin County blue crab landings were most highly correlated with Apalachicola River flows of the previous year and these correlations were positive (Table I). The growout flow with a one-year time lag accounted for the greatest amount of variation in blue crab landings (r^2=0.32, P<0.001; Fig. 3A). The regression analysis of ARIMA residuals (autocorrelation in blue crab landings removed) and growout flows of the previous year was also significant (r^2=0.21; P=0.004). Wakulla County landings were significantly correlated only with Apalachicola flows of the previous year, with the growout flow also accounting for the greatest amount of variation in annual blue crab landings (r^2=0.52, P=0.001; Fig. 3B). The regression analysis of ARIMA residuals and growout flows one year previous was significant (r^2=0.35, P=0.02). The shorter (1973–90) data record for Franklin County landings was more strongly correlated with growout flows with a one-year time lag (r^2=0.49, P=0.001; Fig 3C) than was the full 39-year dataset.

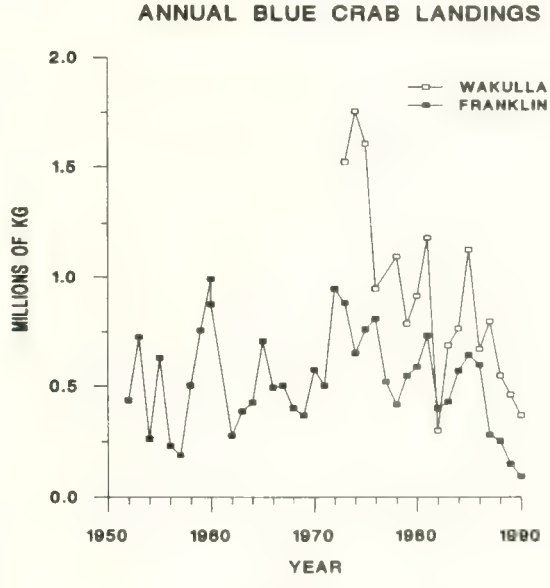

Figure 2

Annual blue crab (*Callinectes sapidus*) landings for Franklin (closed squares) and Wakulla (open squares) Counties in millions of kilograms.

Table 1

R^2 values from regression analyses for Franklin (n=39) and Wakulla (n=17) County blue crab (*Callinectes sapidus*) landings and Apalachicola River flows. All correlations were positive.

Flow parameter	Franklin	Wakulla
no lag period		
7–day low	0.16*	0.12
120–day low	0.14*	0.18
7–day high	0.04	0.07
120–day high	<0.01	<0.01
growout	0.08	0.10
one-year lag		
7–day low	0.25**	0.29*
120–day low	0.21**	0.21
7–day high	0.18*	0.17
120–day high	0.21**	0.31*
growout	0.32***	0.52***

* = $P < 0.05$.
** = $P < 0.01$.
*** = $P < 0.001$.

Monthly and seasonal landings

As expected, the monthly Franklin and Wakulla County blue crab landings (1979–90) exhibited significant autocorrelations for 1- and 12-month time lags. All monthly river flow parameters (minimum, mean, and maximum) also exhibited significant correlations between successive months and with 12-month lags. Correlations between monthly landings and flow parameters (without any adjustments for significant autocorrelations) were positive for time lags of 3, 4, and 5 months. Significant negative correlations were present for flows that lagged 2–4 months behind landings. Correlations that used landings and flow data with the 1- and 12-month autocorrelation effects removed were not significant for either county.

Peak harvests generally occurred between May and September in both counties. There were also no significant correlations between the seasonal (three-

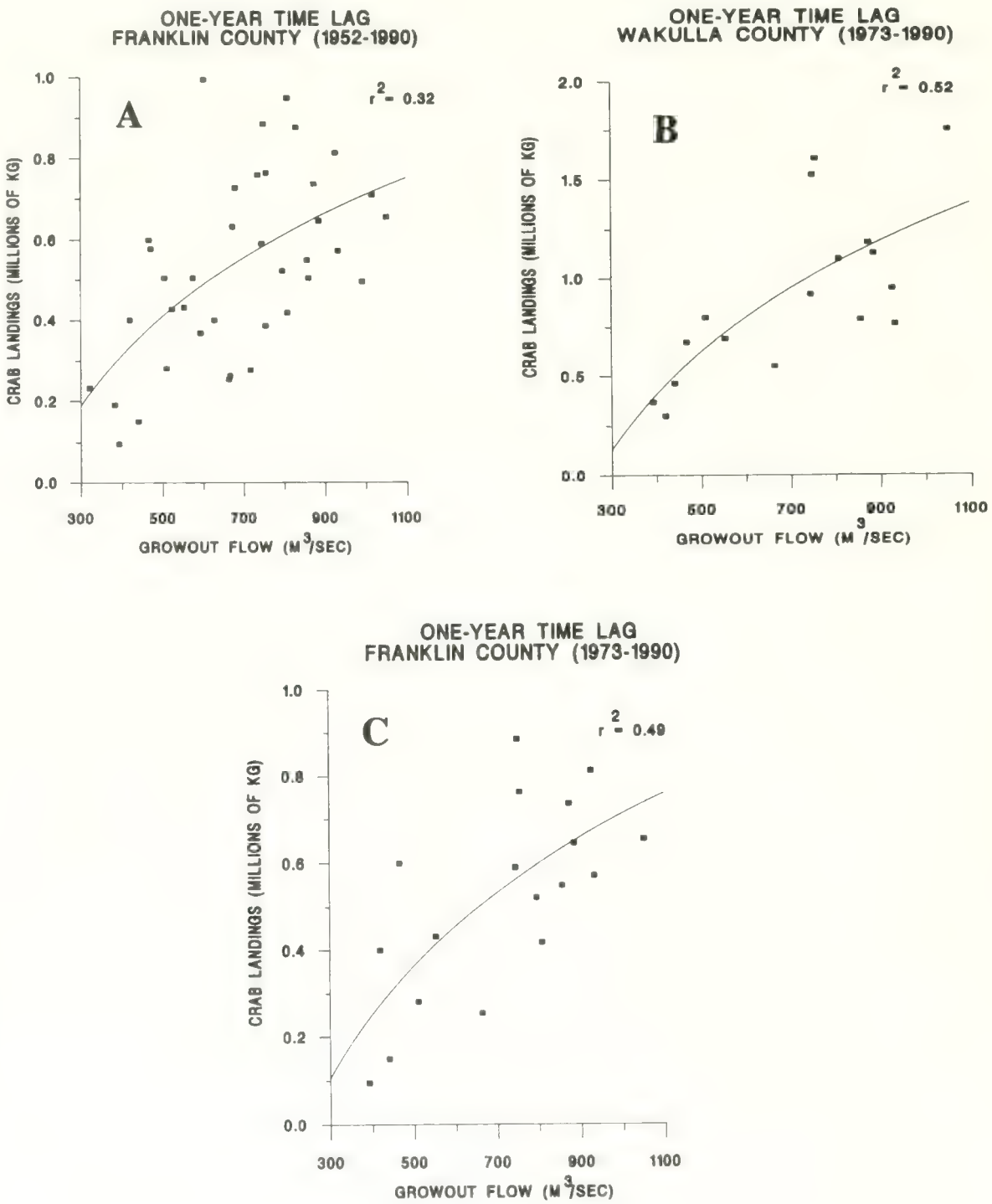

Figure 3

Apalachicola River growout (flows m^3/sec, mean flow from September through May) plotted against the following year's (**A**) Franklin County blue crab landings (1952–90), (**B**) Wakulla County blue crab landings (1973–90 excluding 1977), and (**C**) Franklin County blue crab landings (1973–90). Flow data were log transformed in the statistical analyses.

month average) flow and landings data with autocorrelations removed. The timing of peak monthly harvests was not related to the magnitude of the annual harvests.

Regional analysis

Given the close geographical proximity of the five rivers (Fig. 1) used in the multiple regression analyses, significant correlations between annual flow parameters may be expected among the rivers. Apalachicola River annual mean flows, although significantly correlated with other river flows (except the St. Marks), had the lowest correlations with the other drainages (Table 2).

Significant correlations with blue crab landings were more common for Apalachicola River flows than for any other north Florida river tested (Table 3). Franklin County landings were correlated only with Apalachicola flows, whereas Wakulla County and west coast landings were also correlated with Suwannee and Ochlockonee flows, respectively (Table 3). These significant univariate correlations incorporated a one-year time lag.

The Franklin County multivariate regression model included Apalachicola and Ochlockonee minimum flows of the previous year (r^2=0.45, P<0.001; Table 4). The Wakulla multivariate model accounted for the most variation in blue crab landings (r^2=0.64; Table 4) and included Apalachicola mean and Ochlockonee minimum flows of the previous year. The west coast multivariate model with a one-year time lag included Apalachicola maximum and Ochlockonee minimum and mean flows (r^2=0.53; Table 4).

The only significant multivariate model that included parameters with and without time lags was for west coast landings, which used both no-lag Suwannee minimum flows and Apalachicola maximum flows of the previous year (r^2=0.49). Analyses that examined associations between Apalachicola River flow and west coast landings with Franklin and Wakulla County landings removed were not significant.

Discussion

Several consistent results appeared in the correlations of annual blue crab landings with Apalachicola

Table 2

Pearson correlation matrix of annual mean river flows for all possible combinations of five north Florida rivers.

	Apalachicola	Ochlockonee	St. Marks	Econfina	Suwannee
Apalachicola	1.00				
Ochlockonee	0.59**	1.00			
St. Marks	0.32	0.77**	1.00		
Econfina	0.50*	0.76**	0.64**	1.00	
Suwannee	0.60**	0.93**	0.77**	0.79**	1.00

* = $P < 0.01$.
** = $P < 0.001$.

Table 3

Univariate correlations between Wakulla, Franklin, and west coast blue crab (*Callinectes sapidus*) landings and the river flows from five north Florida drainages (Suwannee, Econfina, St. Marks, Ochlockonee, and Apalachicola) with a one-year time lag. Signs of the correlations are given in parentheses.

Region		Correlation	r^2	P
Franklin	Apalachicola minimum	(+)	0.31	0.001
	Apalachicola mean	(+)	0.25	0.004
	Apalachicola maximum	(+)	0.14	0.039
Wakulla	Apalachicola minimum	(+)	0.29	0.031
	Apalachicola mean	(+)	0.38	0.010
	Suwannee minimum	(+)	0.30	0.028
West Coast	Apalachicola mean	(+)	0.15	0.035
	Apalachicola maximum	(+)	0.26	0.004
	Ochlockonee minimum	(-)	0.22	0.009

Table 4

Multiple regression results for Franklin, Wakulla, and west coast landings of blue crabs (*Callinectes sapidus*) with a one-year time lag incorporated into the analyses. The independent variables are the five river drainages listed in Table 3. Listed below are the signs of the correlations in parentheses, Student's t-statistics, and associated P-values.

Region	Variable	t	P	r^2
Franklin	Apal. min (+)	4.38	<0.001	0.45
	Och. min. (-)	−2.68	0.012	
Wakulla	Apal. mean (+)	4.57	0.001	0.64
	Och. min. (-)	−3.05	0.009	
West Coast	Apal. max. (+)	2.99	0.006	
	Och. mean (+)	3.12	0.004	0.53
	Och. min. (-)	−2.61	0.015	

River flows. Statistically significant correlations were positive and primarily restricted to a time lag of one year, indicating higher flows were associated with higher blue crab landings the following year and lower flows with poorer landings the next year. The mean flow during the growout period (September through May) of the previous year was the most highly correlated flow parameter with blue crab landings in both counties.

A number of explanations are consistent with the observation that more fresh water (within a certain range) was associated with higher blue crab landings the following year. Greater freshwater inflows reduce estuarine salinities, thereby increasing the area of suitable habitat in the middle, and perhaps lower, estuary where juvenile blue crabs can forage and develop (Livingston et al., 1976; Perry, 1984). Increases in low salinity habitat may reduce predation by marine species on juvenile blue crabs. Greater freshwater flows may also broaden an estuary's signal to offshore female migrants and/or megalopae, thus increasing the potential recruitment population base (Perry and Stuck, 1982; Mense and Wenner, 1989). In addition, higher inflows carry more detrital and nutrient matter (Mattraw and Elder, 1982), which may either directly or indirectly enhance food availability.

In both Franklin and Wakulla counties, flows below approximately 600 m^3/sec appear more closely related to the following year's landings than higher growout flows, i.e., the regression equation fits the data better at the low end of the flow spectrum (Fig. 3). Several factors may explain this phenomenon. Food availability may limit blue crab production at flows below a certain level but may not be limiting at flows above this level and, therefore, crab productivity is not influenced by further increases in flow. Prey limitation at low flows may also lead to cannibalism, further limiting blue crab population size (Lipcius and Van Engel, 1990).

The finding that more recent years produce a stronger correlation between blue crab landings and river flows was also observed in Georgia (Rogers et al., 1990[5]). Total discharges from September to May (growout period) of five Georgia rivers were positively correlated with landings (r^2>0.8). Shorter time periods (the most recent 14 and 19 years of landings statistics) produced better correlations with flow than the full period of record (37 years). The authors concluded increased fishing pressure in more recent years resulted in only one year class being fished, and, thus, environmental effects were more obvious on a single year class in the shorter dataset. Similarly, that more recent landings for Franklin County were more highly correlated with Apalachicola River flows than landings for the longer 39-year period may reflect a trend toward harvesting a single year class.

The significant 1- and 12-month time lags in Franklin and Wakulla County reflect similarities in catches between successive months and a seasonal component, respectively. The 12-month autocorrelation indicates that trends in landings occur at the same time of year (e.g., summer peaks) and should not be confused with an annual autocorrelation, which is indicative of a similarity in harvests between entire years. The positive correlations between unadjusted monthly flow and landings data correspond to the summer peak in blue crab landings following 3–5 months after the spring peak in flows, and low winter landings following low late-summer and fall flows. The negative correlations with 2–4 month time lags reflect fall low flows following peak summer harvests and high spring flows occurring after low winter harvests. The absence of significant correlations between monthly landings and flows, once these data were adjusted to remove seasonal autocorrelations, indicates that residual (non-seasonal) variation in monthly flows is unrelated to the non-seasonal variation in monthly landings.

Livingston (1991) found a positive contemporaneous correlation between monthly Apalachicola River flows and blue crab abundances in trawl surveys conducted from 1972 to 1985. This finding corresponds to high juvenile abundances during high-flow months. The positive correlation in the present study between monthly flows and blue crab landings 3–5 months later may reflect the maturation of juveniles into adults in the summer, and thus the observed time lag in the correlation.

The majority of the Apalachicola-Chattahoochee-Flint basin is in Georgia and is subject to different climatic conditions than are the other north Florida rivers examined, which may explain the relatively small correlations between Apalachicola River flows and flows on these other rivers. Georgia rainfall is more strongly correlated with Apalachicola River flows than Florida rainfall (Meeter et al., 1979). A consistent and important finding of the multivariate regression analyses was that Apalachicola flows were more highly correlated with Franklin, Wakulla, and Florida west coast landings of the next year than any other river drainage tested. Regressions comparing Apalachicola flows to west coast landings, after Franklin and Wakulla County landings were removed, were not significant, suggesting the influence of the Apalachicola drainage is restricted primarily to Franklin and neighboring Wakulla County. Thus, there was no evidence supporting the hypoth-

esis of mass blue crab spawning near Apalachicola Bay and larval transport down the gulf coast of Florida via the loop current (Oesterling and Evink, 1977).

Several studies have addressed factors that influence interannual variation in blue crab abundance, primarily concentrating on larval and post-larval recruitment (reviewed in Lipcius and Van Engel, 1990). Lipcius and Van Engel (1990) found high interannual, seasonal, and spatial variation in blue crab abundances in a 17-year fishery-independent dataset collected in the Chesapeake Bay. They observed that years with high blue crab abundances appeared to be dominated by the previous year class because peak catches occurred in the summer. Years with low abundances had peak abundances in the fall, suggesting the dominance of the new year class. This observation supports the contention that variation in recruitment plays a major role in determining interannual fluctuations. No interaction between annual abundance and seasonal peak catch was apparent for the Franklin or Wakulla County blue crab landings, which may indicate either the true absence of such a relation, the inadequacies of using fishery statistics, or a difference in growth rates between the two regions that invalidates the use of the same analysis. Interestingly, the fishery-independent trawl data from the Chesapeake were significantly (r^2=0.33) correlated with the commercial landings data.

The influence of physical factors on blue crab abundances has been documented in other areas, such as a positive relationship between blue crab landings and freshwater inflows in Georgia (Rogers et al., 1990[5]), an inverse relation between salinity and juvenile blue crab abundances on the Texas coast (More, 1969), and a positive relation between blue crab productivity and vegetated area in the Gulf of Mexico (Orth and van Montfrans, 1990). The positive correlation between blue crab landings and Apalachicola River flows of the previous year provides additional evidence of the importance of freshwater inflows to juvenile blue crabs.

Apalachicola River flows have a significant impact on estuarine productivity, as indicated by commercial harvests of oysters (Wilber, 1992) and blue crabs. Although statistical correlations do not indicate the causal mechanisms underlying these associations, the river's influence on estuarine salinities as a mediating factor is deserving of further examination. Undoubtedly, the Apalachicola River affects estuarine biota via mechanisms other than salinity (Livingston, 1991). Factors such as the transport of nutrients and organic matter, however, are unlikely to result in a significant correlation between low flows and oyster harvests two years later, unless food limitation is only measurably important for newly settled oyster spat. In addition, the majority of nutrient and detrital transport from the river occurs during high flow periods in the spring (Mattraw and Elder, 1982). There was no evidence that above-average flows were associated with either oyster or blue crab productivity. In both fisheries, flows on the low end of the spectrum were most significantly associated with landings. These significant correlations were positive and incorporated time lags, suggesting estuarine conditions during low minimum flow periods were not favorable for juveniles of either species.

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Literature cited

Funicelli, N. A.
1984. Assessing and managing effects of reduced freshwater inflow to two Texas estuaries. *In* V. S. Kennedy (ed.), The estuary as a filter, p. 435–446.

Lipcius, R. N., and W. A. Van Engel.
1990. Blue crab population dynamics in Chesapeake Bay: variation in abundance (York River, 1972–1988) and stock-recruit functions. Bull. Mar. Sci. 46:180–194.

Livingston, R. J.
1983. Resource atlas of the Apalachicola estuary. Florida Sea Grant College Publication No. 55, 64 p.
1991. Historical relationships between research and resource management in the Apalachicola River-estuary. Ecological Applications 1(4):361–382.

Livingston, R. J., G. J. Kobylinski, F. G. Lewis III, and P. F. Sheridan.
1976. Long-term fluctuations of epibenthic fish and invertebrate populations in Apalachicola Bay, Florida. Fish. Bull. 74(2):311–321.

Mattraw, H. C., and J. F. Elder.
1982. Nutrient and detritus transport in the Apalachicola River, Florida. U.S. Geol. Surv. Water-Supply Pap. 2196–C.

Meeter, D. A., R. J. Livingston, and G. C. Woodsum.
1979. Long-term climatological cycles and popula-

tion changes in a river-dominated estuarine system. *In* R. J. Livingston (ed.), Ecological processes in coastal and marine systems. Marine Science 10:315–338.

Mense, D. J., and E. L. Wenner.
1989. Distribution and abundance of early life history stages of the blue crab, *Callinectes sapidus*, in tidal marsh creeks near Charleston, South Carolina. Estuaries 12:157–168.

More, W. R.
1969. A contribution to the biology of the blue crab (*Callinectes sapidus* Rathbun) in Texas, with a description of the fishery. Texas Parks Wildl. Dep. Tech. Ser. 1:1–31.

Oesterling, M. L., and G. L. Evink.
1977. Relationship between Florida's blue crab population and Apalachicola Bay. *In* R. J. Livingston and E. A. Joyce (eds.), Proceedings of the conference on the Apalachicola drainage system; 23–24 April 1976, Gainesville, Florida. FL Mar. Res. Pub. 26:101–121.

Orth, R. J., and J. van Montfrans.
1990. Utilization of marsh and seagrass habitats by early stages of *Callinectes sapidus*: a latitudinal perspective. Bull. Mar. Sci. 46:126–144.

Perry, H. M.
1984. A profile of the blue crab fishery of the Gulf of Mexico. Gulf State Mar. Fish. Comm. No. 9, 80 p.

Perry, H. M., and K. C. Stuck.
1982. The life history of the blue crab in Mississippi with notes on larval distribution: proc. blue crab colloquium; 18–19 October 1979, Biloxi, Mississippi. Gulf States Mar. Fish. Comm. 7:17–22.

Steele, P.
1982. A synopsis of the biology of the blue crab *Callinectes sapidus* Rathbun in Florida: proc. blue crab colloquium; 18–19 October 1979, Biloxi, Mississippi. Gulf States Mar. Fish. Comm. 7:29–35.

Wilber, D. H.
1992. Associations between freshwater inflows and oyster productivity in Apalachicola Bay, Florida. Estuarine, Coastal and Shelf Sciences 35:179–190.

Wilkinson, L.
1990. SYSTAT: the system for statistics. SYSTAT, Inc. Evanston, IL, 676 p.

Oocyte maturation in Hecate Strait English sole (*Pleuronectes vetulus*)

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English sole, *Pleuronectes vetulus*, is an important component of the bottom trawl fishery in Hecate Strait, British Columbia, Canada. It is a small-mouthed flounder that feeds on sedentary invertebrates associated with sandy substrate and is most common at depths of 80–150 m (Hart, 1973). The species is characterized by moderate growth (k=0.22), mortality (M=0.20) and longevity (20 years) (Fargo, 1993). It recruits to the fishery at an age of four years, which is roughly equivalent to the age of sexual maturity (Ketchen, 1956; Tyler et al., 1987[1]). Most of the exploited population is under 12 years of age (30–45 cm in length) (Fargo, 1993). Results from tagging studies (Ketchen, 1956; Fargo et al., 1984) and analysis of landing statistics and age composition data (Fargo, 1993) indicate that a single stock exists in Hecate Strait.

Since 1955, abundance for this stock has fluctuated, primarily because of changes in recruitment (Fargo, 1993). Factors influencing recruitment for this stock are poorly understood. Ocean temperature and circulation have been found to influence spawning time and oocyte maturation for the stock off the Oregon coast (Kruse and Tyler, 1989). These authors postulated that 1) the rate of gonadal development for English sole was inversely related to summer bottom temperatures in the same manner as is somatic growth, and 2) spawning was delayed by rapid increases in bottom temperature caused by upwelling. In Hecate Strait, where Ekman transport is weak, these temperature changes may be brought about by the fall transition when strong winds from the south cause mixing of the warm surface waters to depths of 150 metres (Dodimead, 1980[2]). Relatively little information exists on spawning time and egg development for the Hecate Strait stock. We investigated oocyte growth and development to examine the length of the oocyte maturation period and the time and duration of spawning for the English sole stock in Hecate Strait.

Materials and methods

Samples of English sole ovaries were obtained from research cruises and at ports-of-landing from commercial vessels between November 1987 and November 1990. The fish were caught with bottom trawls at five locations throughout Hecate Strait (PMFC Areas 5C-D, Table 1, Fig. 1). Length-stratified samples were collected to ensure that ovaries were obtained throughout the size range of fish collected. For each collection we attempted to sample fifteen sexually mature fish from each 5-cm length interval over a range of 30–50 cm, though this was not always possible. The minimum size fish (30 cm) from which an ovary was dissected corresponds to the length at first maturity for this stock (Ketchen, 1956; Tyler et al., 1987[1]). Total length and the condition of maturity for each fish sampled was recorded. The right ovary was then removed and preserved in a buffered formalin-saline solution (Foucher et al., 1987[3]). Sampling methods have been described in previous reports (Foucher et al., 1987[3]; Tyler et al., 1987[1]). A list of ovary samples examined is given by sample type and month in Table 1.

Preserved ovaries were prepared for histological examination by soaking in Davidson's fixative for approximately 24 hours. Subsequently, tissue sections were dissected from the anterior portion of the ovary (which contained the greatest amount of eggs), embedded in paraffin wax, sectioned at 5 µ, stained with haematoxylin and counterstained with eosin (Yasutake and Wales, 1983).

Oocyte diameter was measured with a light microscope calibrated

[1] Tyler, A. V., J. Fargo, R. P. Foucher, and J. B. Lucas. 1987. Studies on the reproductive biology of Pacific cod and English sole in Hecate Strait from the cruise of the FR/V *W.E. Ricker*, November 25–29, 1986. Can MS. Rep. Fish. Aquat. Sci. 1937, 43 p.

[2] Dodimead, A. J. 1980. A general review of the oceanography of the Queen Charlotte Sound-Hecate Strait-Dixon Entrance region. Can. MS. Rep. Fish. Aquat. Sci. 1574, 248 p.

[3] Foucher, R. P., J. Fargo, and J.B. Lucas. 1987. Cruise of the FV *Nucleus*, January 5–17, 1987 to Hecate Strait to study reproductive biology of Pacific cod and English sole. Can. MS Rep. Fish. Aquat. Sci. 1941, 25 p.

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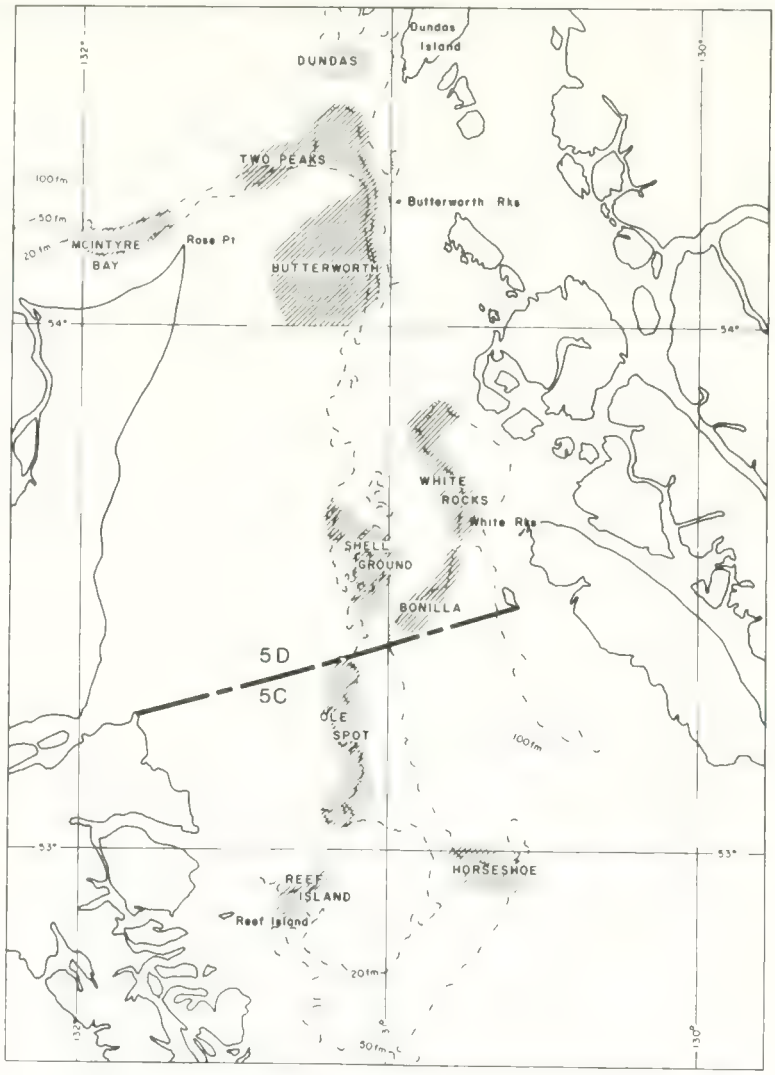

Figure 1

Location of trawling grounds in the study area, Hecate Strait, British Columbia, Canada.

to the nearest 5 μ, or with a projection microscope calibrated to the nearest 4 μ. Three hundred oocytes were measured from at least one fish for every cm length interval for each sample (Table 1). Measurement of 300 oocytes per fish was necessary to provide complete information on the size composition of developing oocytes. Only oocytes that had been sectioned through the nucleus, close to the center of the oocyte, were measured. Mean diameter was estimated as the mean of the minimum and maximum diameters for each oocyte (Foucher and Beamish, 1980). For smaller oocytes (10–20 μ), precision of the measurement was lower because of distortion of the oocyte by surrounding maturing oocytes (Dunn, 1970). A description of the histological stage of oocyte development (Fargo and Sexton, 1991[4]) was also recorded.

We were unable to obtain oocyte measurements from ovaries collected from ripe fish in October and November 1990. These samples were taken from commercial vessels at ports of landing. Ovaries from these samples had combinations of hydrated and non-hydrated oocytes with many burst cells. These fish had been held in chilled seawater for several days prior to sampling, probably exacerbating the state of hydrated oocytes and causing them to burst. Since oocyte diameter data for these samples would have been biased (because most measurable oocytes would not have reached the hydrated state) the slides from these samples were used only to assess the histological stage of the oocytes. This problem did not occur with the November 1987 sample collected at sea on a research vessel.

Prior to statistical testing of the data, we tested oocyte size distributions for normality using the Shapiro-Wilk test. We applied two sample t-tests to test for differences in the mean diameter of previtellogenic and vitellogenic oocytes between months within years and among years. We used linear regression to investigate the relation 1) between fish length and mean oocyte diameter within months and 2) between fish length and mean oocyte diameter at the time of spawning.

Results

Oocyte development

Ovaries were examined from 174 fish (Table 1) caught at five locations in Hecate Strait (Fig. 1). The sampling period encompassed seven different months over three years. Descriptions and micro-

[4] Fargo, J., and T. Sexton. 1991. A quide to the ovarian histology of English sole (*Parophrys vetulus*). Can. MS. Rep. Fish. Aquat. Sci. 2133, 19 p.

graphs of the stages of maturation for English sole oocytes have been summarized by Fargo and Sexton (1991).[4] Examples of oocyte size distributions for fish of different lengths sampled during the same period, August 1988, are presented in Figure 2. For all sizes of English sole collected, we observed the simultaneous presence of only two modes in the oocyte size distributions. The smaller mode (10–150 μ) consisted of previtellogenic oocytes and the larger mode (150–500 μ) of vitellogenic oocytes. No previtellogenic ooctyes >150 μ were observed. The size modes for previtellogenic oocytes were similar among fish ranging in size from 33 to 46 cm. The mode for vitellogenic oocytes shifted to the right (increased) with increasing fish length.

Vitellogenic oocytes increased in size from early summer until they became hydrated prior to spawning in the fall (Fig. 3). We observed no trend in the size composition of previtellogenic oocytes over the same period. As the month of spawning was approached a complete separation between the two modes became apparent. The irregular shape of the modal distribution for vitellogenic oocytes in Figure 3 is caused by combining data for fish of different lengths and developing at different rates. The more normal distribution for this mode during the month of spawning is due to two factors. First, the size range of fish for this sample was smaller than for other samples and, second, egg diameter at the time of spawning was similar for fish of different length. Fargo and Sexton (1991)[4] described the events of oocyte maturation for English sole in detail. Briefly,

Table 1

A summary of ovary samples examined in the study of oocyte maturation in Hecate Strait English sole (*Pleuronectes vetulus*).

Date	Sample type	Location	Length class (cm) (No. ovaries examined)
7–13 January 1987	Research cruise	Two Peaks White Rocks	30–34 (2)
			35–39 (6)
			40–44 (5)
			45–49 (5)
			50–54 (4)
			55–59 (1)
		Total	(23)
19 January 1988	Port sample	White Rocks	30–34 (1)
			35–39 (1)
			40–44 (1)
		Total	(3)
17 March 1987	Research cruise	Horseshoe	30–34 (2)
			35–39 (2)
			40–44 (3)
			45–49 (2)
			50–54 (1)
		Total	(10)
16 March 1988	Port sample	Horseshoe	30–34 (1)
			35–39 (4)
			40–44 (2)
			45–49 (1)
		Total	(8)
May 5 1988	Port Sample	Horseshoe-White Rocks	30–34 (1)
			35–39 (1)
			40–44 (2)
			45–49 (6)
		Total	(10)
6 June 1987	Research cruise	Horseshoe-Bonilla	30–34 (1)
			35–39 (3)
			40–44 (3)
			45–49 (3)
			50–54 (3)
		Total	(12)
2 June 1988	Port sample	Horseshoe	30–34 (1)
			35–39 (3)
			40–44 (3)
			45–49 (3)
			50–54 (2)
		Total	(12)
27 August 1987	Research cruise	Horseshoe	30–34 (1)
			34–39 (7)
			40–44 (5)
			50–54 (1)
		Total	(14)

Table 1 (continued)

Date	Sample type	Location	Length class (cm) (No. ovaries examined)
22 August 1988	Port sample	Horseshoe	30-34 (2)
			34-39 (5)
			40-44 (8)
			45-49 (6)
			50-54 (1)
		Total	(22)
28 August 1990	Port sample	Two Peaks	35-39 (4)
			40-44 (4)
			45-49 (4)
			50-54 (1)
		Total	(13)
27 January 1988	Port sample	Two Peaks-Butterworth	30-34 (4)
			35-39 (2)
			40-44 (3)
			45-49 (1)
			50-54 (1)
		Total	(11)
19 January 1990	Port sample	Horseshoe	30-34 (1)
			35-39 (6)
			40-44 (8)
			45-49 (1)
		Total	(16)
5–6 November 1987	Research cruise	Horseshoe-Butterworth-White Rocks	30-34 (5)
			35-39 (7)
			40-44 (4)
			45-49 (2)
			50-54 (1)
3 November 1990	Port sample	Butterworth	30-34 (1)
			35-39 (1)
			40-44 (2)
			45-49 (1)
			50-54 (1)
		Total	(6)

vitellogenesis occurred when oocytes reached a diameter of about 150 μ. Vacuolization occurred in oocytes ranging from 180 μ to 250 μ Deposition of yolk in the outer cortex occurred in oocytes ranging in size from 200 μ to 430 μ, and hydrated oocytes ranged in size from 375 μ to 550 μ.

We began our investigation of the timing and duration of oocyte maturation by examining the size composition and histological stage of oocytes collected from fish sampled between January and November. Ovaries examined from 68 of 72 fish collected during winter and spring (January 1987–88 and March 1987–88) contained mainly previtellogenic oocytes. The fish examined from the January samples contained previtellogenic oocytes only. Four of 22 fish examined from samples collected during the month of March contained vitellogenic oocytes. Three of these (36–40 cm in length) contained vitellogenic oocytes that were hydrated and translucent (405–429 μ mean diameter). The fourth fish (46 cm in length) contained oocytes that had recently undergone vitellogenesis (mean diameter=230 μ).

Vitellogenesis for most fish occurred in the early summer. In May 1988, we observed vitellogenic oocytes in six of nine fish examined, ranging from 40 to 49 cm in length. All of these oocytes were in the early stages of development, prior to vacuolization, with mean diameters ranging from 174 to 263 μ. Smaller fish (length range 33–42 cm) contained previtellogenic oocytes only . In June (1987, 1988) vitellogenic oocytes, ranging in mean diameter from 178 μ to 269 μ, were present in 23 of 24 fish examined (length range 36–52 cm). Vitellogenic oocytes in one fish of 52 cm were at an advanced stage of development (mean diameter=252 μ), with yolk granules formed in the outer cortex. The relation between mean diameter of vitellogenic oocytes and fish length was not significant for the months of May (1988) and June (1987, 1988) (linear regression, $P>0.1$ for all three, $n=6, 11, 12$)

By August the oocytes in some of the larger fish (45–50 cm) were nearing hydration. Mean diameters for vitellogenic oocytes from fish sampled in August (1987, 1988, 1990) ranged from 226 μ to 429 μ. There were significant, positive linear relationships between fish length and mean oocyte diameter for all of these samples (Table 2, Fig. 4).

The size distributions for previtellogenic and vitellogenic oocytes did not differ significantly (Shapiro-Wilk test, $P<0.05$) from that of the normal distribution for any of the following cases. There was no significant difference in mean diameter of previtellogenic oocytes for the same months across

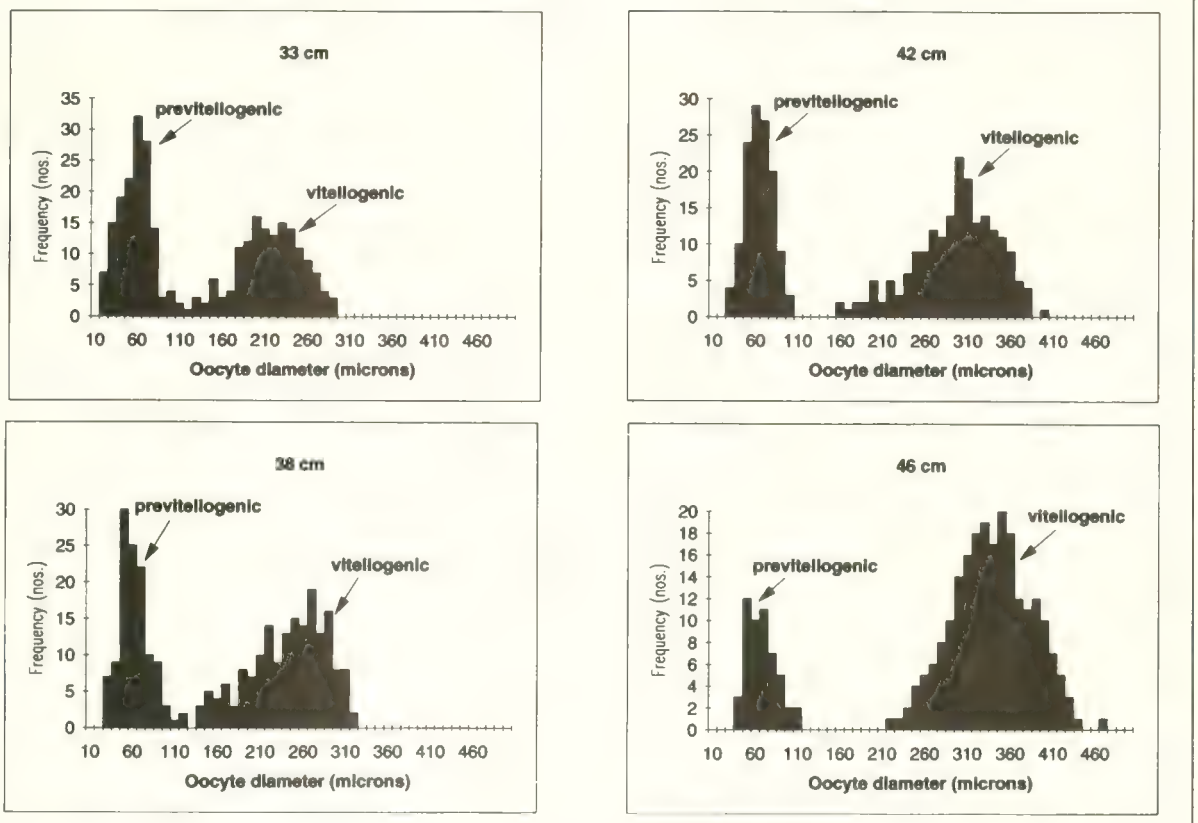

Figure 2

Oocyte size compositions determined from ovary samples collected from Hecate Strait English sole (*Pleuronectes vetulus*) in August 1988.

the two years (Table 3). However, there were significant differences in mean diameter for previtellogenic oocytes among months within both years (Table 4). No obvious trend in mean diameter over time was apparent for previtellogenic oocytes. There were significant differences in the rate of oocyte development between 1987 and 1988 (Table 3). The mean diameter of vitellogenic oocytes in June and August of 1987 was significantly larger than for the same months in 1988, suggesting that vitellogenesis occurred earlier in 1987 than in 1988. There were also significant differences in the mean diameter of vitellogenic oocytes among months within years (Table 5). The mean diameter of vitellogenic oocytes increased significantly, coinciding with advancing oocyte development, between June–November in 1987 and June–October in 1988.

Spawning

Ovaries obtained from spawning fish (October 1988, 1990 and November 1987, 1990) were examined to investigate 1) size-dependent spawning and 2) the relation between fish length and egg diameter at the time of spawning. For the October 1988 sample, we observed the presence of vitellogenic oocytes only in fish smaller than 40 cm. The mean diameter of vitellogenic oocytes in these fish ranged from 287 to 408 μ. Fish ranging in length from 43 to 52 cm contained spent ovaries with previtellogenic oocytes only. Thus, we concluded that the larger fish had spawned prior to the time of the sample collection. In the October 1990 sample, taken two weeks earlier than the 1988 sample, some of the fish larger than 40 cm contained hydrated oocytes while others had spent ovaries with resorbing oocytes, suggesting that they were spawning in early October. Oocytes examined from samples collected in November (1987, 1990) also indicated that larger fish had spawned previous to this time. Fish larger than 42 cm contained only pre-vitellogenic oocytes and there was no sign of resorbing oocytes. Most smaller fish were in spawning condition during this month. Vitellogenic oocytes were present in fish ranging from 30 to 42 cm. Mean diameter ranged from 373 to 483 μ and these oocytes were hydrated and trans-

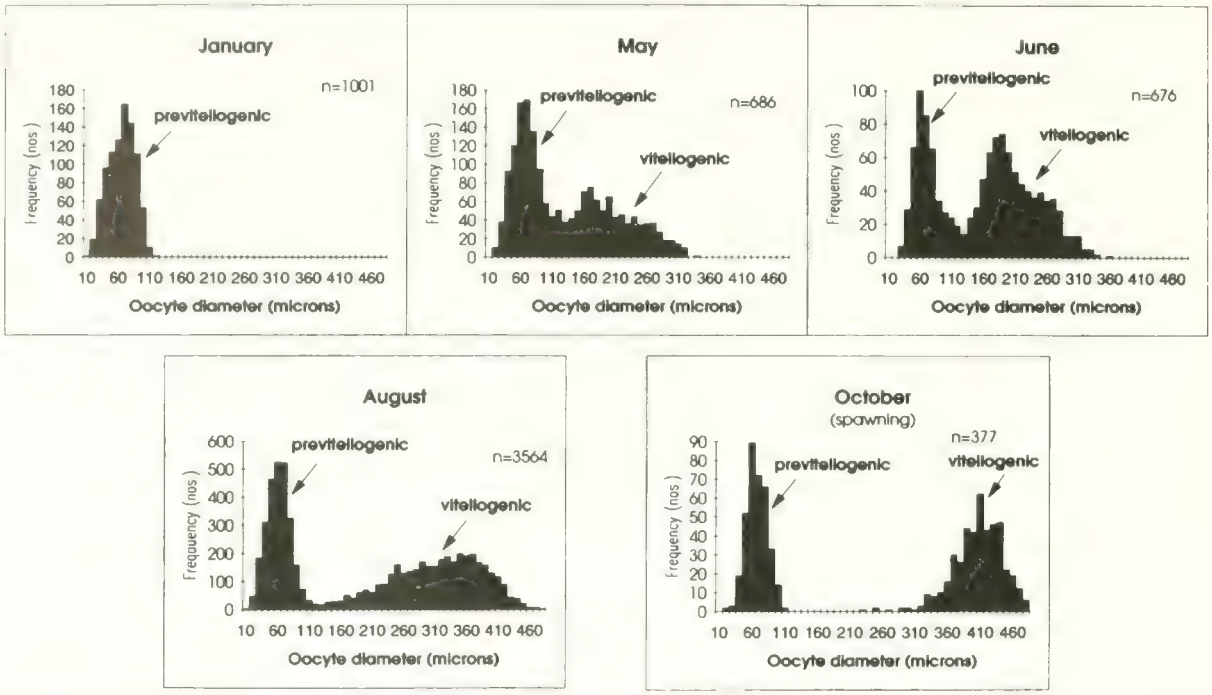

Figure 3

Oocyte size composition determined from ovary samples collected from Hecate Strait English sole (*Pleuronectes vetulus*) during January-October in 1988 (samples combined).

lucent. We then combined all the data on mean egg diameter for spawning fish and there was no relationship between mean egg diameter at the time of spawning (hydrated and translucent) and fish length (linear regression, $P>0.1$, $n=19$).

Table 2

Linear regression statistics for the relationship between vitellogenic oocyte mean diameter and fish length for English sole (*Pleuronectes vetulus*) for the month of August 1987, 1988, and 1990.

Year	Degrees of freedom	*F*-statistic	*P*	Regression equation[1]	*r*
1987	13	10.72	0.007	$Y = 122 + 5.93X$	0.687
1988	20	20.93	<0.0001	$Y = -93 + 9.44X$	0.910
1990	12	44.01	<0.0001	$Y = -237 + 12.6X$	0.724

[1] Y = oocyte mean diameter (μ).
X = total length of fish (cm).

Discussion

Oocyte development

Dunn and Tyler (1969) and Dunn (1970) determined the length of time required for oocyte maturation in winter flounder (*Pleuronectes americanus*). They observed two size modes of previtellogenic oocytes at any particular time. They documented the rate of increase in size for these modes for three consecutive years and concluded that the oocyte maturation period for this species was three years.

We observed only a single mode for both previtellogenic and vitellogenic oocytes in fish sampled during all the months examined in our study. Johnson et al. (1991) reported similar results in their study of Puget Sound English sole. If oocytes produced in year i were spawned in year $i+1$, we would expect to see two size classes of immature oocytes in year $i+1$, corresponding to those oocytes that were produced in year i (large immatures) to be spawned in year $i+1$ and those that were produced in year $i+1$ (small immatures) to be spawned in year $i+2$. The fact that there were no significant differences in the mean diameter of previtellogenic oocytes for the same months in consecutive years (1987–88) suggests that the oocyte maturation period for Hecate Strait English sole is probably one year.

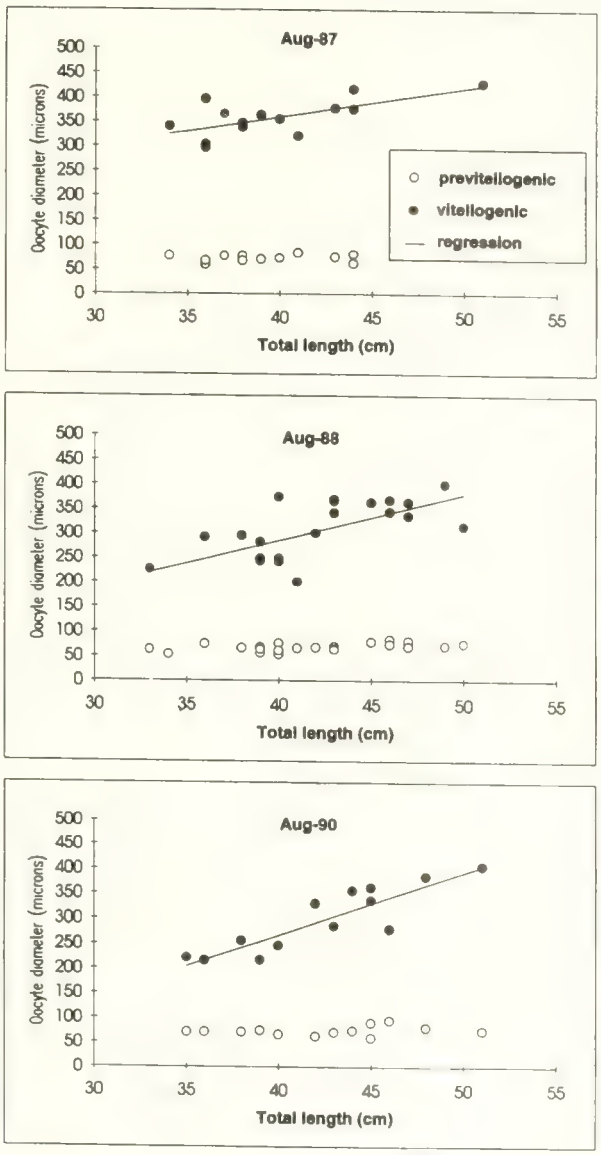

Figure 4

Mean oocyte diameter vs fish length determined from ovary samples collected from Hecate Strait English sole (*Pleuronectes vetulus*) during the month of August, 1987, 1988, and 1990.

We also found no trend in the mean size of previtellogenic oocytes among months within years, contrary to results reported by Dunn and Tyler (1969). One explanation for this is that the recruitment of small immature (previtellogenic) oocytes from the germinal epithelium is a continual process for Hecate Strait English sole. Alternatively, there may be a short time period, following spawning for example, during which previtellogenic oocytes recruit and quickly grow to a size of around 80 μ. Additional work is needed to resolve these possibilities.

Table 3

Results of two sample *t*-tests of mean diameters of previtellogenic and vitellogenic oocytes for English sole (*Pleuronectes vetulus*) determined from samples collected during the same month in 1987 and 1988.

Month and year	*n*	mean diameter (microns)	*P*
previtellogenic			
January 1987	6,264	69.0	
January 1988	1,001	69.4	>0.1
March 1987	1,603	59.2	
March 1988	1,737	59.8	>0.1
June 1987	1,389	72.4	
June 1988	1,132	72.9	>0.1
August 1987	1,812	66.7	
August 1988	2,071	65.8	>0.1
vitellogenic			
June 1988	953	219.1	
June 1988	1,029	203.3	<0.0001
August 1987	1,774	362.1	
August 1988	3,584	318.1	<0.0001

Spawning

In general larger fish produced yolk earlier and spawned earlier than smaller fish. Most of the spawning fish were obtained from samples collected in October and November but there was also evidence of spring (March) spawning for smaller fish. Egg size at the time of spawning did not appear to be dependent on fish length. However, there is some evidence from this study to suggest a possible minimum size limit for eggs at the time of spawning. That is, the difference in the mean diameter of vitellogenic oocytes between smaller and larger fish decreased over time until there was no apparent difference at the time of spawning. Observations made during this study indicate that atresia was not as prevalent for Hecate Strait English sole as that reported for English sole in Puget Sound by Johnson et al. (1991).

Marine fish species show wide variability in the reproductive process, which enables them to mitigate the uncertain conditions in the marine environment (Murphy, 1968; Roff, 1981). English sole demonstrate considerable phenotypic plasticity with regard to spawning. In Hecate Strait the spawning season extends from early fall through the follow-

Table 4

Results of two sample t-tests of the mean diameter (μ) of previtellogenic oocytes in English sole (*Pleuronectes vetulus*) among months for samples collected in 1987 and 1988.

Year and Month	January	March	June	August	November
1987					
January (n=6264, $\bar{x}$=69.0μ)	—	P<0.0001	P<0.0001	P=0.0004	P<0.0001
March (n=1603, $\bar{x}$=59.2μ)	—	—	P<0.0001	P<0.0001	P<0.0001
June (n=1389, $\bar{x}$=72.4μ)	—	—	—	P<0.0001	P<0.0001
August (n=1812, $\bar{x}$=66.7μ)	—	—	—	—	P<0.0001
November (n=4205, $\bar{x}$=63.0μ)	—	—	—	—	—

Year and Month	January	March	May	June	August	October
1988						
January (n=1001, $\bar{x}$=69.4μ)	—	P=0.0009	P<0.0001	P=0.0009	P<0.0001	P<0.0001
March (n=1737, $\bar{x}$=59.8μ)	—	—	P<0.0001	P<0.0001	P<0.0001	P<0.0001
May (n=1609, $\bar{x}$=76.2μ)	—	—	—	P=0.003	P<0.0001	P<0.0001
June (n=1132, $\bar{x}$=72.9μ)	—	—	—	—	P<0.0001	P<0.0001
August (n=2071, $\bar{x}$=65.8μ)	—	—	—	—	—	P<0.0001
October (n=1500, $\bar{x}$=56.9μ)	—	—	—	—	—	—

Table 5

Results of two sample t-tests of the mean diameter (μ) of vitellogenic oocytes in English sole (*Pleuronectes vetulus*) among months for samples collected in 1987 and 1988.

Year and month	June	August	November
1987			
June (n= 953, $\bar{x}$=219.1μ)	—	<0.0001	<0.0001
August (n=1774, $\bar{x}$=362.1μ)	—	—	<0.0001
November (n= 488, $\bar{x}$=413.7μ	—	—	—

Year and month	May	June	August	October
1988				
May (n=191, $\bar{x}$=201.4μ)	—	>0.1	<0.0001	<0.0001
June (n=1029, $\bar{x}$=203.3μ)	—	—	<0.0001	<0.0001
August (n=3584, $\bar{x}$=318.1μ)	—	—	<0.0001	<0.0001
October (n=710, $\bar{x}$=342.1μ)	—	—	—	—

ing spring. Johnson et al. (1991) reported a similar spawning period for Puget Sound English sole as did Kruse and Tyler (1989) in their study of English sole off the Oregon coast. This reproductive strategy may increase the probability of encountering favorable conditions for larval survival by spreading the reproductive effort over the longest possible time span.

Based on our results it is unlikely that cohort-specific spawning occurs as in Pacific herring, *Clupea pallasi* (Ware and Tanasichuk, 1989), and Norwegian Atlantic herring, *Clupea harengus* (Lambert, 1990). However, in view of the relation between oocyte maturation and fish length and the duration of the spawning period, it is possible that first time

spawners spawn at a different time than the rest of the stock. We can suggest no mechanism to account for this and more data are required to corroborate these results.

There is also evidence of interannual variability in oocyte maturation and this process appears to be size-related. Smaller fish matured later and spawned later than larger fish. Our results indicate that the time of peak spawning and the duration of the spawning season are variable from year to year. The results from this study provide baseline information for an investigation of the recruitment biology of this stock.

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We wish to acknowledge John Bagshaw, Serge Villeneuve, Tammy Laberge, Christina Horvath, Tracy Sexton, and Corinne Kikegawa for their aid in preparing the slides for histological examinations and photography of specimens. Ron Tanasichuk and Doug Hay reviewed the manuscript and provided advice regarding the spawning characteristics for the species. The scientific editor and three anonymous reviewers provided a number of suggestions which improved the paper.

Literature cited

Dunn, R. S.
1970. Further evidence for a three year oocyte maturation time in the winter flounder (*Pseudopleuronectes americanus*). J. Fish. Res. Board Canada. 27:957–960

Dunn, R. S., and A. V. Tyler.
1969. Aspects of the anatomy of the winter flounder (*Pseudopleuronectes americanus*) with hypotheses on oocyte maturation time. J. Fish. Res. Board Canada 26:1943–1947.

Fargo, J.
1993. Flatfish. *In* B. M. Leaman and M. Stocker (ed.), Groundfish stock assessments for the west coast of Canada in 1992 and recommended yield options for 1993. Can. Tech. Rep. Fish. Aquat. Sci. 1919:95–131.

Fargo, J, R. P. Foucher, S. C. Schields, and D. Ross.
1984. English sole tagging in Hecate Strait, R/V G.B. REED, June 6–24, 1983. Can. Data Rep. Fish. Aquat. Sci. 427, 49 p.

Foucher, R. P., and R. J. Beamish.
1980. Production of nonviable oocytes by Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 37:41–47.

Hart, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180, 740 p.

Johnson, L. L, E. Casillas, M. S. Myers, L. D. Rhodes and O. P. Olson.
1991. Patterns of oocyte development and related changes in plasma 17–B estradiol, vitellogenin and plasma chemistry in English sole *Parophrys vetulus* Girard. J. Exp. Mar. Biol. Ecol. 152: 161–185.

Ketchen, K. S.
1956. Factors influencing the survival of the lemon sole (*Parophrys vetulus*) in Hecate Strait, British Columbia. J. Fish. Res. Board Canada, 13(5): 647–694.

Kruse, G. H., and A. V. Tyler.
1989. Exploratory simulation of English Sole (*Parophrys vetulus*) recruitment mechanisms. Trans. Am. Fish. Soc. 118:101–118.

Lambert, T. C.
1990. The effect of population structure on recruitment in herring. J. Cons. int. Explor. Mer 47:249-255.

Murphy, G. I.
1968. Pattern in life history and the environment. Am. Nat. 102:391–403.

Roff, D. A.
1981. Reproductive uncertainty and the evolution of iteroparity: why don't flatfish put all their eggs in one basket? Can. J. Fish. Aquat. Sci. 38:968–977.

Ware, D. M., and R. Tanasichuk.
1989. Biological basis of maturation and spawning waves in Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 46(10):1776–1784.

Yasutake, W. T., and J. H. Wales.
1983. Microscopic anatomy of salmonids: an atlas. Fish. Wild. Ser. U.S. Dep. Int. Res. Pub. 150, 189 p.

Estimation of weight-length relationships from group measurements

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Catch sampling provides data that are basic to fisheries research and is often an important component of research budgets. Samplers typically select fish randomly, measure length, remove ageing structures, and determine sex for each individual. In many schemes for sampling commercial (e.g., Sen, 1986; Tomlinson, 1971) and survey catches (e.g., Gunderson and Sample, 1980), sample weight is needed to expand the sample results to the total catch. Individual weights are usually not needed to satisfy the main objectives. Often only the aggregate weight of the sample is taken to save time, and if at sea, to avoid difficult logistics. While sampling costs are easily justified by program objectives, scientists frequently use the data for additional research.

Investigators often use weight-length relations to study possible correlations between condition of fish and environmental factors or population density (e.g., Patterson, 1992). A literature search revealed only two previous developments of methods of estimating weight-length relations from samples of individual lengths and aggregate weights (WLRAW). Cammen (1980) used a general nonlinear regression program from the BMDP package (Dixon, 1983) as a WLRAW method. He tested the method with simulated data and compared the results of regression using unweighted observations to using observations weighted by the inverse of sample weights, and with various estimates made when individual weights were known. Since the data were simulated, assuming a multiplicative error term, it would have been more appropriate to use the inverse of sample weight squared for weighting. The nonlinear method produced good fits to the simulated data, and weighted parameter estimates were closer to the true values than unweighted estimates. Damm (1987) developed two nonlinear WLRAW methods. One method is a biased approximation, and his report indicated that the other method did not always produce estimates of the parameters.

In this note I describe a new WLRAW method, compare it with Cammen's method, explore error term characteristics, and describe bootstrap estimates of confidence limits of estimates. The methods of Damm (1987) were not studied because his biased approximation method requires as much calculation as my new method and his other method does not always work.

Methods

The relation between expected weight and length of an individual fish is usually assumed to be the power equation,

$$E(W_i) = \alpha L_i^{\beta} \qquad (1)$$

Where W_i = weight of fish i,
α = parameter,
L_i = length of fish i,
β = parameter.

For the new WLRAW method I modeled the weight-length relationship as

$$\overline{W}_j = \frac{\alpha}{n_j} \sum_{i=1}^{n_j} \left(L_{ij}^{\beta}\right) + \varepsilon_j, \qquad (2)$$

where $\overline{W}_j$ = average weight of fish in sample j,
n_j = number of fish in sample j,
L_{ij} = length of fish i in sample j,
ε_j = error term for sample j,
j = 1, . . . , T,
T = number of samples.

I assumed that error was additive because under field conditions much of the error was due to limits to the accuracy in measurement of sample weights. Because the dependent variable in Equation 2 was a sample average, its variance should contain a component which is proportional to the inverse of n_j. Thus in the new estimation procedure, I weight each observation by n_j to stabilize the variance. I made the assumption that, after weighting by sample size, error was random and independent of j.

The new method treated estimation of parameters of (Eq. 2) as a separable least-squares problem (Seber and Wild, 1989). For a trial value of β (β'), γ_j was calculated for each sample,

$$\gamma_j = \left(\sum_{i}^{n} L_{ij}^{\beta}\right) / n_j. \qquad (3)$$

With the new notation, Equation 2 becomes

$$\overline{W}_j = \alpha' \gamma_j + \varepsilon_j. \qquad (4)$$

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I then obtained an estimate of α (α') corresponding to β' by using the standard least squares linear regression with zero intercept method. I used a nonlinear least squares procedure to obtain the estimate of β ($\hat{\beta}$). This procedure was analogous to finding the transformation, $L_{ij}^{\hat{\beta}}$, that minimized the sum of squares about the linear regression (Eq. 4). Using this procedure, I estimated brackets for ensuring that the searching range included $\hat{\beta}$ with the procedure MNBRAK (Press et al., 1989). Then I used the iterative procedure BRENT (Press et al., 1989) to obtain the final estimate. BRENT uses parabolic interpolation to minimize the sum of squares as a function of β'. Convergence is assumed when the procedure does not change the value of β' more than a tolerance specified by the user. As previously stated, observations were weighted by n_j to stabilize the variance. I implemented the WLRAW method in double precision using Sun FORTRAN for a Sun SPARC2 work station.

Bootstrap approximations of confidence intervals about the line were calculated for the new method. The literature contains a variety of bootstrap methods proposed to approximate confidence intervals (e.g., DiCiccio et al., 1992). I used the nonparameteric BC_a method of Efron (1987) because it often produces good results and is relatively easy to use.

BC_a stands for accelerated bias corrected bootstrap confidence intervals. Efron (1987) showed that, in the parametric case, the method is approximately correct if a transformation to a normally distributed variable exists. The transformation does not need to be known and the variance does not need to be constant. While the correctness of the BC_a has not been mathematically proven for nonparametric cases, such as the WLRAW, Efron (1987) stated, "...empirical results look promising." The BC_a confidence limits of an estimate of parameter θ, $\hat{\theta}$, are

$$IBS(N(z[\alpha])) \le \theta \le IBS(N(z[1-\alpha])). \qquad (5)$$

$IBS(P)$ is the value of θ that corresponds to the percentile P of the cumulative bootstrap frequency distribution. $N(Z)$ is the percentile of the cumulative normal probability distribution that corresponds to the standard deviate Z. $z[\alpha]$ is given by Efron (1987) as

$$z[\alpha] = z_0 + \frac{z_0 + z^{(\alpha)}}{1 - a\left(z_0 + z^{(\alpha)}\right)}. \qquad (6)$$

$z^{(\alpha)}$ is the standard deviate that corresponds to the α percentile of the normal cumulative distribution. z_0 is the standard deviate of the normal cumulative distribution that corresponds to the percentile that corresponds to $\hat{\theta}$ in the cumulative bootstrap frequency distribution. Efron (1987) called z_0 the *bias constant*. Efron called a the *acceleration constant*. It is related to the skewness of the bootstrap frequency distribution. Efron gave the following approximation for a:

$$a \approx \frac{1}{6}\left[\frac{(\sum_{j=1}^{J} U_j^3)}{(\sum_{j=1}^{J} U_j^2)^{3/2}}\right], \qquad (7)$$

where $U_j = \dfrac{\hat{\theta}_j^{(\Delta)} - \hat{\theta}}{\Delta}$

$\hat{\theta}^{(\Delta)}$ = estimate of θ when jth sample has a very small amount of extra weighting (Δ).

If a and z_0 are zero, then Equation 7 becomes the percentile method that is the most frequently used bootstrap method in the fisheries literature (e.g., Sigler and Fujioka, 1988).

I chose to approximate 90% confidence bands rather than 95% or 99% bands because 90% nonparametric bootstrap intervals tend to perform better than intervals that cover a wider portion of the distribution (Efron, 1988). Following the advice of Efron, I used 1,000 bootstrap replicates.

Cammen (1980) used the general nonlinear regression program of BMDP to estimate the parameters of Equation 2, except that he assumed that the error term is multiplicative and used total sample weight instead of average weight as the dependent variable. The BMDP program uses the Gauss-Newton algorithm. I used the same algorithm in the nonlinear regression program of the SAS package (SAS Institute Inc., 1989) on a Sun SPARC2 to compare parameter estimates and execution times with the new method. Since the correct error model is not known, I also estimated the parameters using no weighting and weight set to $1/\overline{W}_j, 1/\overline{W}_j^2$, $n_j/\overline{W}_j$, and $n_j/\overline{W}_j^2$, and compared asymptotic standard errors of the parameter estimates. The new estimation procedure is simpler than the Gauss-Newton approach because it searches for the least squares by iteratively changing the value of one parameter instead of two.

I used data collected on chilipepper rockfish (*Sebastes goodei*) by a cooperative landing sampling program of the California Department of Fish and

Game and National Marine Fisheries Service to examine utility of the WLRAW method. Samplers collected two groups of fish from each sampled landing. For each group a container that holds 22.7 kg of fish was filled with fish regardless of species. Then the sampler obtained total group weights to the nearest lb (0.45 kg) for each species and the total length of each fish was measured to the nearest mm. I converted weights to kg. I changed lengths to decimeters to minimize potential scaling problems in the computations. Before using the WLRAW method, I combined groups within a landing because they may not be independent.

I first used data for all months during 1991 from all ports between Morro Bay and Crescent City, California, to develop, test, and time the software. Results of the test runs are described briefly in the Results and Discussion section. More detailed results are presented for a more typical application of the method. Investigators are more likely interested in results from a smaller number of samples taken from more restrictive scales of time and area than from data sets like the one used in the preceding example. I used data for chilipepper rockfish taken during July and August 1991 from Morro Bay to illustrate use of the method.

Results and discussion

The data from all ports consisted of measurements from 7,687 fish taken in 186 samples. The procedure required 1.6 seconds, compared with 18.8 seconds for the Gauss-Newton method. The Gauss-Newton and new methods produced parameter estimates that were identical to six decimal places. Predicted weights were very close to the results of Phillips (1964), who used data from individually measured fish. Sums of squares plotted against β' indicated that there were no local minima. Residuals were not related to weight, indicating that the additive error assumption is correct. Sometimes transformation of β' to $\ln(\beta')$ when estimating parameters of power equations avoids problems due to curvature (Ratkowsky, 1983). Transformation was tried and parameter estimates were identical to the results when β' was not transformed. When β' was transformed, the procedure required more time to complete, so the transformation was not used.

Data were available for 583 fish taken from 13 samples taken in Morro Bay, during July and August 1991. There were no strong trends between the residual and expected weight (Fig. 1). There was a tendency for absolute values of residuals to be negatively correlated with the number of fish in a sample (Fig. 2A). The tendency was reduced when residuals were multiplied by $\sqrt{n_j}$, as expected under the assumption that variance is proportional to the inverse of sample size (Fig. 2B). Also, n_j produced the lowest asymptotic standard errors of the parameter estimates of the six weighting factors explored (Table 1). The results shown in Table 1 and Figures 1 and 2 indicated that the additive error model with weighting by n_j was appropriate for these data. Bootstrap estimates of standard error using the new method were higher than asymptotic estimates using the Gauss-Newton method. The bootstrap and asymptotic normal confidence intervals were narrow and similar within the range of most observed average weights but diverged when expected weight was greater than 0.75 kg even though individual fish of larger size occurred in many of the samples (Table 2). The bootstrap confidence intervals were skewed at the larger sizes. However, the bootstrap estimates of absolute bias were less than 0.01 kg except they were –0.01 kg for 450-mm fish and –0.02 kg for 500-mm fish. All estimates of the absolute value of a were about 0.015, which indicated that a could have been ignored for this set of data.

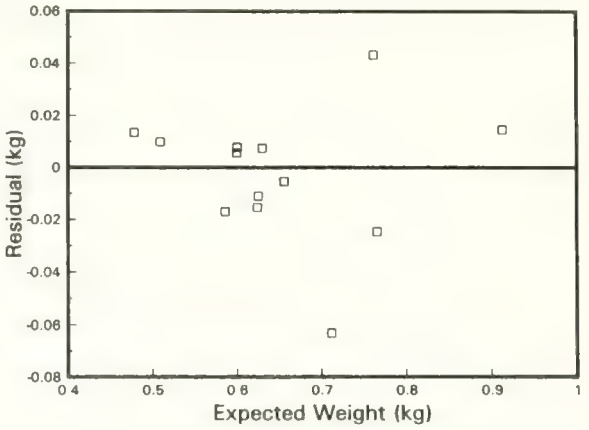

Figure 1

Residual of average weight (kg) as a function of expected weight (kg) for chilipepper rockfish (*Sebastes goodei*) collected in samples taken from Morro Bay during July and August 1991.

The new WLRAW method performed well. Good fits to the data were obtained and the residuals agreed with the assumptions. Approximate confidence limits indicated that precise estimates of expected weight are obtained with a small number of samples under field conditions for sizes of fish within the range of most observed average weights. The method is fast when used on a work station or on a modern personal computer. The new method is 10 times faster than using the Gauss-Newton ap-

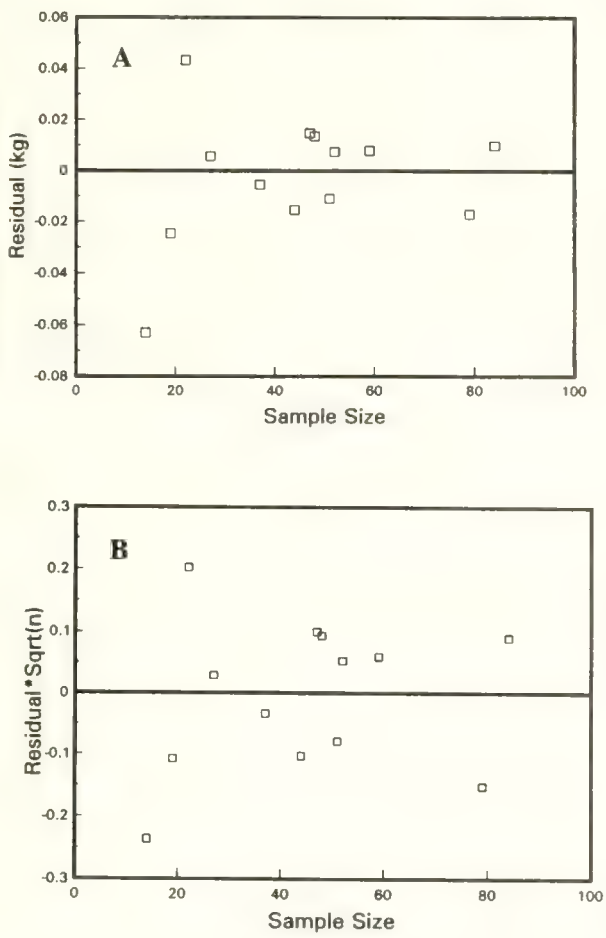

Figure 2

(**A**) Residual of average weight (kg) as a function of sample size for chilipepper rockfish (*Sebastes goodei*) collected in samples taken from Morro Bay during July and August 1991. (**B**) Residual multiplied by $\sqrt{n_j}$ as a function of sample size.

proach with a standard statistical package. Some of the difference is probably due to the overhead involved with using the statistical package. When computationally intensive methods such as bootstrapping are used, time saved by using the new method is significant.

The widening confidence limits for expected weights beyond the range of most observed average weights indicated use of expected weights beyond the observed range is extrapolation and should not be done. This also applies to comparison of parameter estimates from different sets of data. If the range of observed average weights differ much among the data sets, comparison of parameter estimates is not meaningful. Estimates of the two parameters of the weight-length relation are highly correlated even when individuals are weighed and standard linear regression is used (Lenarz, 1974). Thus, regardless of the type of data or statistical

Table 1

Estimates of standard errors of parameter estimates of weight-length model for chilipepper rockfish (*Sebasted goodei*) collected from Morro Bay during July and August 1991. The Gauss-Newton method was used with observations weighted by six factors to estimate the parameters, and the new method with n_j as the weighting factor. Asymptotic standard errors are shown for the Gauss-Newton method and bootstrap standard errors for the new method. Coefficients of variation of the parameter estimates are shown in parentheses.

Weighting factor	Standard error α	Standard error β
Gauss-Newton method		
none	0.0028 (0.30)	0.2159 (0.07)
n_j	0.0019 (0.21)	0.1489 (0.05)
$n_j/\overline{W}_j$	0.0020 (0.20)	0.1528 (0.05)
$n_j/\overline{W}_j^2$	0.0022 (0.20)	0.1547 (0.05)
$1/\overline{W}_j$	0.0030 (0.29)	0.2129 (0.07)
$1/\overline{W}_j^2$	0.0032 (0.28)	0.2069 (0.07)
New method		
n_j	0.0046 (0.50)	0.2211 (0.07)

Table 2

Expected weights for chilipepper rockfish (*Sebastes goodei*) collected from Morro Bay during July and August 1991, and 90% confidence about the line. Confidence limits were approximated using the bootstrap BC_a (bootstrap) and the asymptotic normal methods (normal). Expected weights were calculated from the estimated weight-length relation (0.0091819 Length$^{3.1758673}$).

Total length (dm)	Expected weight (kg)	Confidence limits: Normal Lower (kg)	Normal Upper (kg)	Bootstrap Lower (kg)	Bootstrap Upper (kg)
3.00	0.30	0.28	0.32	0.28	0.33
3.50	0.49	0.47	0.51	0.47	0.50
3.75	0.61	0.60	0.62	0.60	0.62
4.00	0.75	0.74	0.76	0.73	0.76
4.50	1.09	1.04	1.14	0.99	1.12
5.00	1.52	1.42	1.63	1.31	1.61

procedure, I recommend comparison of weight-length relations among data sets by comparison of expected weights of fish at sizes within the range of observed average weights common to all data sets of interest.

The results of this study suggest that an additive error term is more appropriate than a multiplicative error term for modeling weight-length relations. Most previous studies have assumed multiplicative error, which is implied when the log-log transformation is used to estimate parameters of the model from individually measured fish by linear regression. The multiplicative error assumption has not been demonstrated correct even when data are available from fish weighed individually. While good fits to data are usually obtained under the multiplicative assumption, if the assumption is not valid, statistical inferences may be erroneous. Pienaar and Thomson (1969) assumed that the error term was additive for their data and discussed statistical aspects of the assumption. Further examination of the error term form would be interesting.

Copies of the FORTRAN code used in this study are available from the author.

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Literature cited

Cammen, L. M.
1980. Estimation of biological power functions from group measurements. Can. J. Fish. Aquat. Sci. 37:716–719.

Damm, U.
1987. The estimation of weight at length from the total weight and the length distribution of a sample. ICES CM 1987/D:16, 9 p.

DiCiccio, T. J., M. A. Martin, and G. A. Young.
1992. Fast and accurate approximate double bootstrap confidence intervals. Biometrika 79(2): 285–95.

Dixon, W. J.
1983. BMDP statistical software. Univ. California Press, Berkeley, 733 p.

Efron, B.
1987. Better bootstrap confidence intervals. J. Am. Statist. Assoc. 82(397):171–185.
1988. Bootstrap confidence intervals: good or bad? Psychol. Bull. 104(2):293–6.

Gunderson, D. R., and T. M. Sample.
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42 (3–4):2–16.

Lenarz, W. H.
1974. Length-weight relations for five eastern tropical Atlantic scombrids. Fish. Bull. 72:848–851.

Patterson, K. R.
1992. An improved method for studying the condition of fish, with an example using Pacific sardine *Sardinops sagax* (Jenyns). J. Fish Biol. 40: 821–831.

Phillips, J. B.
1964. Life history studies on ten species of rockfish (genus Sebastodes). Calif. Dep. Fish Game Fish Bull. 126, 70 p.

Pienarr, L. V., and J. A. Thomson.
1969. Allometric weight-length regression model. J. Fish. Res. Board Canada 26:123–131.

Press, W. H., B. P. Flannery, S. A. Teukolsky and W. T. Vetterling.
1989. Numerical recipes the art of scientific computing (FORTRAN version). Cambridge Univ. Press, Cambridge, 702 p.

Ratkowsky, D. A.
1983. Nonlinear regression modeling. Marcel Dekker, NY, 276 p.

SAS Institute Inc.
1989. SAS/STAT® User's guide, version 6, 4th edition, Vol. 2. SAS Institute Inc., Cary, NC, 846 p.

Seber, G. A., and C. J. Wild.
1989. Nonlinear regression. J. Wiley & Sons, NY, 768 p.

Sen, A. R.
1986. Methodological problems in sampling commercial rockfish landings. Fish. Bull. 84:409–421.

Sigler, M. F., and J. T. Fujioka.
1988. Evaluation of variability in sablefish, *Anoplopoma fimbria*, abundance indices in the Gulf of Alaska using the bootstrap method. Fish. Bull. 86:445–452.

Tomlinson, P. K.
1971. Some sampling problems in fishery work. Biometrics 27:631–41.

Spiny lobster recruitment and sea level: results of a 1990 forecast

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A relation between recruitment to the fishery and sea level for the spiny lobster *Panulirus marginatus*, in the Northwestern Hawaiian Islands, was supported by data from 1985 through 1990 (Polovina and Mitchum, 1992). A forecast of future recruitment was made based on projected sea levels (Polovina and Mitchum, 1992). This note updates that forecast with two more years of data.

Fishery data from 1985 to 1990 indicated considerable interannual variation in recruitment strength of spiny lobster, *Panulirus marginatus*, between the two principal fishing grounds (Necker Island and Maro Reef), although separated by about 700 km (Fig. 1; Polovina and Mitchum, 1992). Recruitment strength variation between the two fishing areas was measured as the ratio of the commercial landings from Maro Reef divided by the combined commercial landings from Necker Island and Maro Reef. A strong correlation was observed between this measure of recruitment strength at Maro Reef and the sea level gradient along the Northwestern Hawaiian Islands, advanced by four years (Polovina and Mitchum, 1992). The sea level gradient was measured as the difference in sea level between tide gauges at French Frigate Shoals, southeast of Maro Reef, and Midway Island, northwest of Maro Reef. A high proportion of the commercial landings came from Maro Reef following a steep gradient, while relatively few spiny lobsters were caught at Maro Reef following a flat gradient. The four-year lag is based on the minimum legal harvest size which, for the spiny lobster is about three years old, after benthic settlement. Prior to benthic settlement, the larvae are planktonic for about one year.

Since sea level gradient appears to lead recruitment to the fishery by four years, the relation can provide up to a four-year forecast. Based on data through 1990, it was forecast that in 1991 recruitment to the fishery at Maro Reef would be weak but would recover in 1992 relative to recruitment at Necker Island (Fig. 2). The 1991 and 1992 fishery data show this forecast correct (Fig. 2), although the fishery for the entire Northwestern Hawaiian Islands was relatively weak in 1992. Thus, while sea level gradient index does forecast the relative strength of recruitment at Maro Reef, it is not, by itself, an index of absolute recruitment strength.

It has been argued that sea level gradient measures the strength of the Subtropical Counter Current, which appears to intersect the Hawaiian ridge as three narrow eastward flowing bands at 20, 24, and 26 degrees north latitude (Polovina and Mitchum, 1992; White and Walker, 1985). Recent studies of *P. marginatus* larval distribution find a relatively high abundance of late stage larvae consistently present near lat. 26°N, and tracks from Argos drifter buoys drogued at 30 m indicate buoy entrainment along lat. 26°N.[1] These results provide some additional support to our original hypothesis that a positive relationship exists between the strength of the Subtropical Counter Current and local larval survival, retention, and recruitment to the fishery at Maro Reef (Polovina and Mitchum, 1992).

Literature cited

Polovina, J. J., and G. T. Mitchum.
1992. Variability in spiny lobster *Panulirus marginatus* re-

[1] Polovina, J.J., and R.B. Moffitt. In review. The spatial and temporal distribution of the larvae of the spiny lobster (*Panulirus marginatus*) in the Northwestern Hawaiian Islands.

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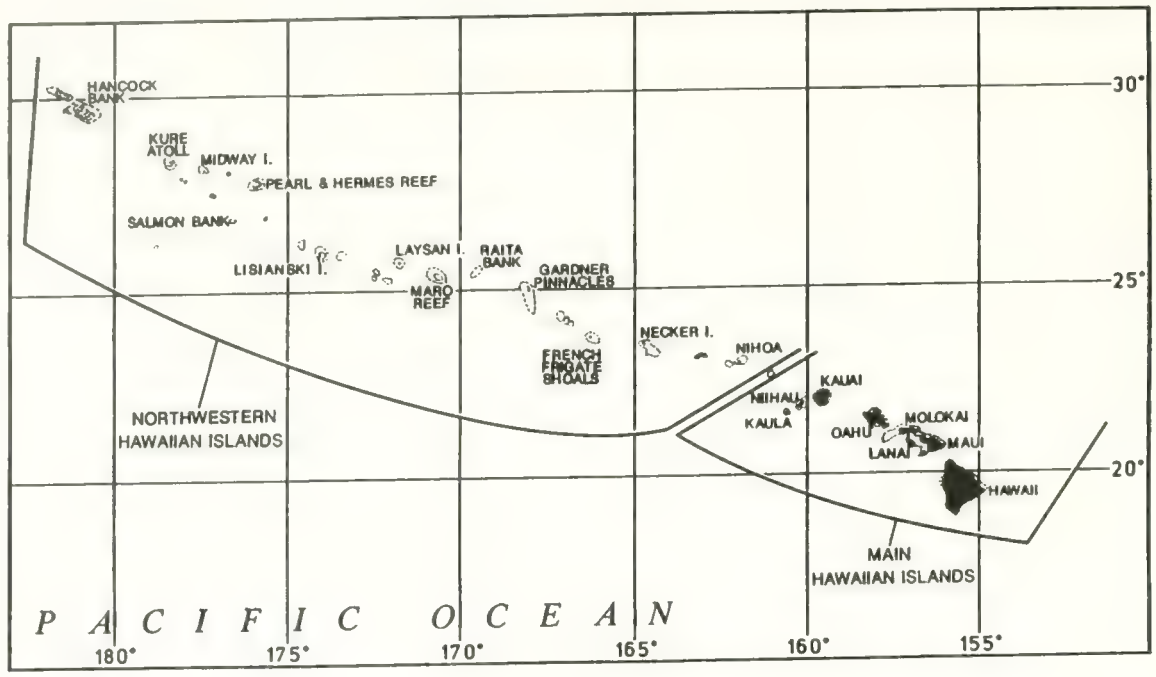

Figure 1
The Hawaiian Archipelago.

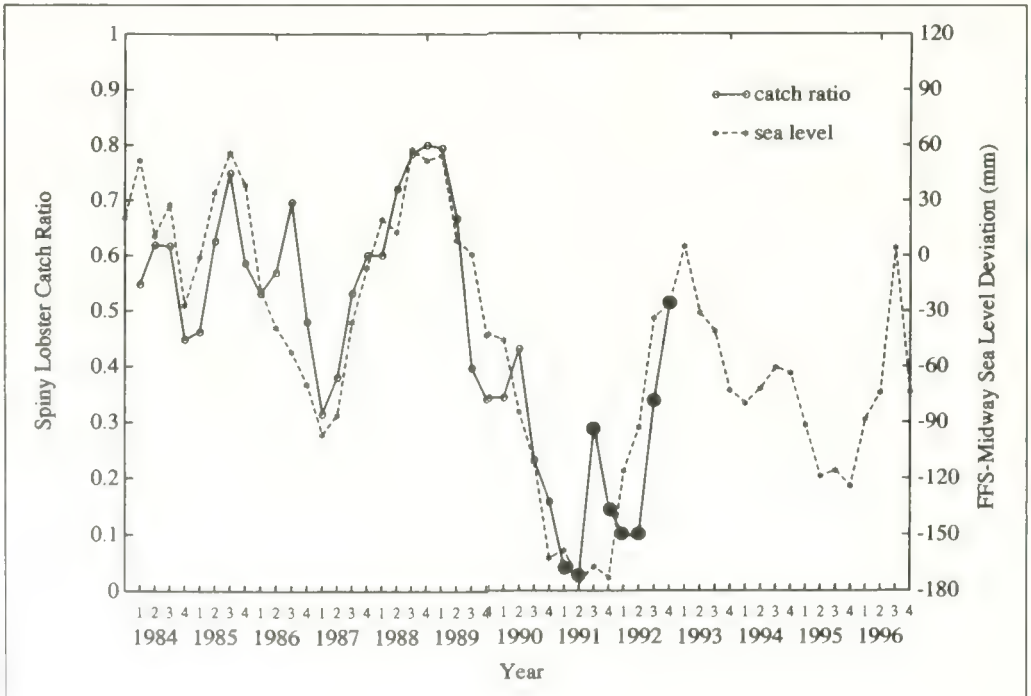

Figure 2
Three-quarter moving average of the ratio of quarterly landings of spiny lobster, *Panulirus marginatus*, at Maro Reef to quarterly landings at Maro Reef and Necker Island (bold line), 1984–92. Solid dots are values of the catch ratio since the 1990 forecast. Overlayed is the 3-quarter moving average of French Frigate Shoals (FFS)-Midway sea level deviation advanced by four years (dashed line), 1980–92.

cruitment and sea level in the Northwestern Hawaiian Islands. Fish. Bull. 90:483–493.

White, W. B., and A. E. Walker.

1985. The influence of the Hawaiian Archipelago upon the wind-driven subtropical gyre in the Western North Pacific. J. Geophys. Res. 90 C4:7061–7074.

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Distribution and relative abundance of the blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean

Errata

(1)

Bigelow, Keith A.

Age and growth of the oceanic squid *Onychoteuthis borealijaponica* in the North Pacific
Fish. Bull. 92(1):13-25

Figure 5 should read as shown below.

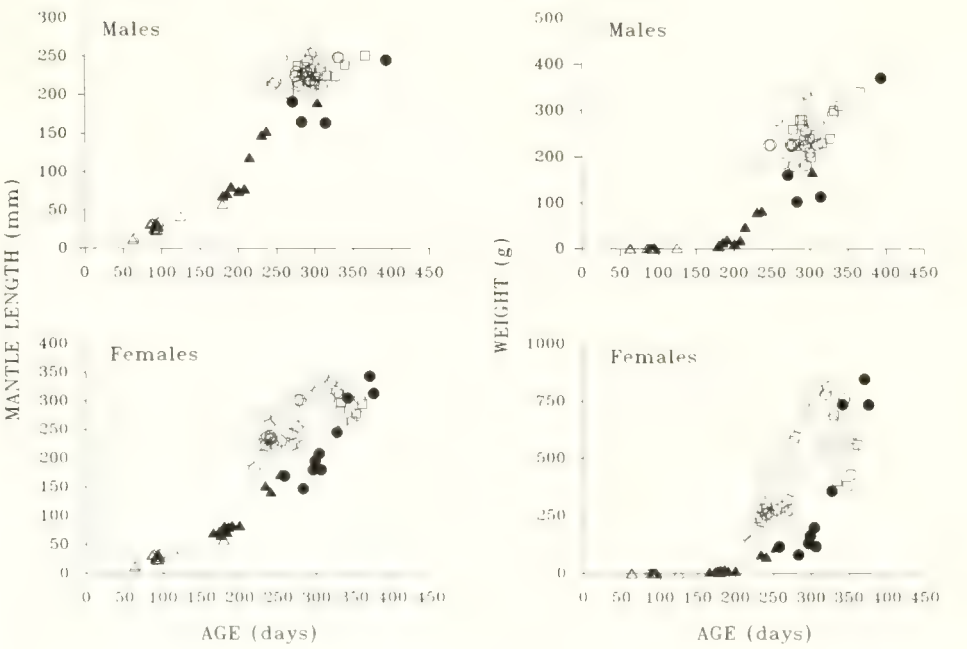

Figure 5

Relation between age (determined by number of increments within statoliths) and mantle length (mm) and weight (g) for male and female *Onychoteuthis borealijaponica*. Western North Pacific 1990 (open circles), central North Pacific 1990 (closed circles), central North Pacific 1991 (closed triangles = juveniles-subadults, open triangles = unknown sex), and eastern North Pacific 1990 (open squares).

(2)

Perryman, Wayne L., and Morgan S. Lynn

Examination of stock and school structure of striped dolphin (*Stenella coeruleoalba*) in the eastern Pacific from aerial photogrammetry
Fish. Bull. 92(1):122-131

Figures 3, 4, and 7, and Tables 1, 2, and 3 show an incorrectly typeset species name for striped dolphin. The correct name should read striped dolphin, *Stenella coeruleoalba*.

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Abstract.— Eggs of walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Alaska, were reared at three temperatures: 3.8°, 5.7°, and 7.7°C. Development was divided into 21 stages. A piecewise regression model with midpoints of each stage describes the relation between time to each stage of development and temperature. Preserved eggs of each stage are described, illustrated, and photographed. Midpoint of hatch was 393 hours at 3.8°C, 303 hours at 5.7°C, and 234 hours at 7.7°C. Mean length of larvae at hatch increased linearly with temperature.

We compared rate of development, time to 50% hatch, and morphological development with other studies of walleye pollock eggs. Rate of development and time to 50% hatch were similar among populations of eastern North Pacific walleye pollock. Western North Pacific walleye pollock required longer incubation times than eastern North Pacific walleye pollock. Morphological development of Shelikof Strait eggs differs from development of western North Pacific walleye pollock eggs: optic vesicles, myomeres, eye lenses, heart, and otic capsules appear earlier than in Shelikof Strait eggs, and eye pigment appears later. The differences in development may be exacerbated by the condition of the eggs in which they were examined (e.g. preserved vs. live). Developmental differences between stocks are discussed with the conclusion that model components for egg mortality and spawning biomass must be based on specimens collected in the area of interest.

Embryonic development of walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska*

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Walleye pollock, *Theragra chalcogramma*, is the most abundant member of the family Gadidae in the subarctic Pacific Ocean and Bering Sea, supporting the largest single-species commercial fishery in the world (Megrey, 1991). In the Gulf of Alaska, Shelikof Strait is the principal spawning area (Kendall and Picquelle, 1990) and has been the site of intensive research to understand processes leading to recruitment variability of walleye pollock (Schumacher and Kendall, 1991).

Age determination of fertilized eggs is a basis for investigating biotic and abiotic impacts on the earliest life-history stage and thus for understanding interannual variability in walleye pollock recruitment. Age of walleye pollock eggs has been crucial to several studies. Egg mortality and spawning biomass are estimated by modeling age-specific egg abundance over time (Picquelle and Megrey, 1993; Bates[1]). Patterns in horizontal or vertical distribution and abundance of walleye pollock eggs in the western Gulf of Alaska have been described by grouping developmental stages into broad age groups (Kendall and Kim, 1989; Kendall and Picquelle, 1990).

Egg age is an independent variable in the models used to estimate egg production and mortality. Therefore, increasing the accuracy in measuring egg ages should improve estimates of these values. In past studies, walleye pollock eggs have been incubated in the laboratory to develop temperature-specific equations that estimate duration of development or age of the eggs, to describe morphological development, to observe effects of light on egg buoyancy and hatching rate, and to obtain larvae for experiments (Table 1). Although these incubation studies provide pertinent data on ontogeny of walleye pollock, none can be used with accuracy to determine age of eggs

[1] Bates, R. D. 1987. Estimation of egg production, spawner biomass, and egg mortality for walleye pollock, *Theragra chalcogramma*, in Shelikof Strait from ichthyoplankton surveys during 1981. U.S. Dep. Commer., NOAA, Nat. Mar. Fish. Serv., Northwest Alaska Fish. Cent., 7600 Sand Point Way N.E., Bin C15700, Bldg. 4, Seattle, WA 98115-0070. Proc. Rep. 87-20, 192 p.

* Contribution 0148 of the Fisheries Oceanography Coordinated Investigations, NOAA, Seattle.

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Table 1

Summary of *Theragra chalcogramma* egg incubation studies.

Reference	Temperature (°C)	Source and region	Stages[1]	Regression equation	Morphological description	Illustrations	Photographs
Gorbunova, 1954	3.4, 8.2 (means)	western Pacific Ocean	None	No	Yes	Yes	No
Yusa, 1954	6.0–7.0	Ishikari Bay, Japan	27[2]	No	Yes	Yes	Yes
Hamai et al., 1971	2.4–2.5, 6.5–6.7, 9.9–10.1, (means)	Funka Bay, Japan	4	Stage-specific equation to predict age (d) at any stage	No	No	No
Hamai et al., 1974	5.0 (mean)	Funka Bay, Japan	6	No	No	No	No
Matarese 1983, unpubl.[3]	5.0	N. Gulf of Alaska	21	Stage-specific equation to predict age (h) at any stage[4]	No	No	No
Haynes and Ignell, 1983	2.0, 5.0, 6.0, 8.0, 11.0	Stephens Passage, SE Alaska	7	General equation to predict age (h) at any stage	No	No	No
Nakatani and Maeda, 1984	–1.0, 0.0, 2.0, 4.0, 7.0, 10.0, 13.0	Funka Bay, Japan	5	To 50% hatch	No	No	No
Paul, 1984, unpubl.[5]	5.0	N. Gulf of Alaska	21	No	No	No	No
Bailey and Stehr, 1986	5.6, 8.5	Puget Sound, Washington	None	No	No	No	No
Olla and Davis, 1993	6.0	Shelikof Strait, Alaska	None	No	No	No	No

[1] Prior to hatch.
[2] Reported as intervals of time.
[3] A. C. Matarese, Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE., Seattle, WA 98115.
[4] In Bates 1987 (Footnote 1).
[5] A. J. Paul, University of Alaska Fairbanks, Institute of Marine Science, Seward Marine Center Lab, P.O. Box 730, Seward, AK 99664.

from Shelikof Strait. Eggs need to be obtained from the study area and incubated at a range of temperatures occurring in the area. Categorizing the continuous process of egg development into a large number of stages should increase the precision of the egg-age estimate.

The first objective of our study was to incubate Shelikof Strait walleye pollock eggs at the mean water temperature for Shelikof Strait, bracketing that temperature to include upper and lower extremes. Egg development times were used to produce a stage duration table and a regression model to estimate egg age based on water temperature and developmental stage. Morphological development is described for 21 developmental stages. These descriptions are accompanied by illustrations and photographs to facilitate identification of body structures and stage hallmarks.

The second objective was to compare our rates of egg development to other walleye pollock incubation studies. Morphological development is included in this comparison.

Methods

Incubation

Adult walleye pollock were collected with a rope trawl off Cape Kekurnoi (57°42.5'N, 155°16.2'W) in Shelikof Strait, Alaska, on 7 April 1989 from the NOAA research vessel *Miller Freeman*. Eggs from one female and milt from three or four males were hand stripped into glass petri dishes, gently mixed, and left undisturbed for one minute. Eggs were then rinsed, transferred to 3°C (surface water temperature) seawater in glass jars (3.8 L), and held two hours. Floating eggs with a perivitelline space were assumed to be fertilized (Blaxter, 1969; Alderdice, 1988). Viable eggs were poured into eighteen 0.5-L jars filled with 3°C seawater. Eggs were not counted but apportioned similarly among the jars at a concentration of about one egg/mL. Six capped jars were held in each of three water bath incubators onboard the *Miller Freeman*. Initial incubation temperatures were set to include the range of temperatures in the area. Mean water temperature at depths of 150–200 m in Shelikof Strait, where most eggs are found (March–May) (Kendall and Kim, 1989), is 5°C; extremes of 3.6° and 5.9°C have been reported (Reed and Schumacher, 1989). Incubators were sealed to minimize light and movement and placed in separate refrigerators adjusted to 3°, 5°, and 7°C. One-half of the water in the jars was replaced every day with seawater of the same temperature. Eggs were preserved in phosphate buffered formalin (5%)[2] or Stockard's solution[3] (Velsen, 1980). Stockard's solution cleared the chorion and darkened embryonic tissue, easing examination of embryonic development. Phosphate buffered formalin did not darken embryonic tissue as much as Stockard's solution, yielding better definition of some structures like somites and otic capsules. Live, newly hatched larvae were measured (standard length in millimeters) and preserved (5% buffered formalin). Detailed examination and morphological description of embryos were completed after eggs were returned to the laboratory.

During the first 24 hours after fertilization, eggs were sampled at 2–3 hour intervals. After 24 hours, intervals were increased to about 6 hours. When an interval was less or greater than 6 hours, the subsequent sampling time was adjusted to return to the original 6–hour schedule. Data were not recorded for three sampling times late in development because intervals were inadvertently extended to 12 hours (236, 258, and 282 hours).

At each interval, 10 to 50 eggs were sampled from one jar per incubator; only one jar was sampled to ensure there would be enough eggs and larvae left to sample near the end of the incubation period. Jars were sampled in rotation throughout the duration of the experiment until no eggs remained. When eggs began to hatch, all jars were checked and newly hatched larvae were removed in addition to eggs scheduled to be sampled. Dead eggs were removed from the designated sample jar at each interval. Water bath temperatures were recorded for every sampling interval. Frequent opening of refrigerators during the initial short sampling intervals increased temperatures in the refrigerators despite thermostat adjustments. Water bath temperatures stabilized after 48 hours to 3.8°, 5.7°, and 7.7°C.

Morphological descriptions

Eggs were examined with the aid of a dissecting microscope (6–50× magnification) and described according to a 21-stage scheme adapted from Naplin and Obenchain (1980) (Table 2). Morphological terms follow Trinkaus (1951) with one exception: the term "blastodisc," in this paper, includes the germinal area from the time of cytoplasm polarization until embryonic shield formation (Markle and

Table 2

Stages of embryonic development of *Theragra chalcogramma* (adapted from Naplin and Obenchain, 1980).

Stage	Developmental stage
1	Precell
2	2 cell
3	4 cell
4	8 cell
5	16 cell
6	32+ cell
7	Blastodermal cap
8	Early germ ring
9	Germ ring 1/4 down yolk
10	Germ ring 1/2 down yolk
11	Germ ring 3/4 down yolk
12	Late germ ring
13	Early middle (blastopore closure)
14	Middle middle (appearance of pigment)
15	Late middle (tail bud thickens)
16	Early late (tail bud lifts from yolk)
17	Tail 5/8 around yolk
18	Tail 3/4 around yolk
19	Tail 7/8 around yolk
20	Full circle around yolk
21	Tail 1-1/8 around yolk

[2] 50 mL 37% formaldehyde, 4.0 g sodium phosphate monobasic, 6.5 g sodium phosphate dibasic, made up to 1 L with distilled water.

[3] 50 mL 37% formaldehyde, 40 mL glacial acetic acid, 60 mL glycerin, and 850 mL distilled water.

Waiwood, 1985, in part). Eggs preserved in Stockard's solution were photographed with a Nikon F2 camera fitted with a PB6 200-mm bellows extension and a 24-mm 1:2.8 reverse-mounted lens. This configuration produced a 47× magnification. Reflected light was supplied by two synchronized flash units. Other photographs (stages 5 and 6) were taken with a single-lens reflex adapter (0.32×) on a Wild M-8 dissecting microscope with transmitted light. At 50×, the phototube and adapter increased magnification to 66×.

Analysis

Endpoint, midpoint, and duration of stage (in hours) were estimated for eggs incubated at each temperature. For stages 1–20, stage endpoint was determined by the presence of two stages during a sampling time; if stages n and $n+1$ were present, the time at which the eggs were sampled was considered a transition and therefore the endpoint for stage n. If there was no transition, the endpoint for stage n was the midpoint between the last sampling time during which stage-n eggs were present and the first time stage-$n+1$ eggs were observed. Duration and midpoint of stage n were determined as

$$\text{Duration Stage } n = \text{Endpoint Stage } (n) - \text{Endpoint Stage } (n-1);$$

$$\text{Midpoint Stage } n = \text{Endpoint Stage } (n-1) + \frac{\text{Duration Stage } n}{2}.$$

Endpoint of stage 21 was the sampling interval when the last embryo had hatched. With the midpoints and time of 50% hatch, a piece-wise least-squares linear regression model (SAS, 1985) was derived to estimate age (hours) of eggs at a specific stage incubated at any temperature within the limits of this experiment.

Differences in mean lengths of larvae hatched from the three temperature groups were analyzed by a Student-Newman-Keuls test. Lengths of larvae hatching at stages 20 and 21 were analyzed by a two-way analysis of variance (ANOVA) by using stage and temperature.

We chose five representative developmental stages and compared time to midpoint of each stage among incubation studies. Comparison with Hamai et al. (1971, 1974) was possible for only three stages. We grouped data on time to 50% hatch into western and eastern North Pacific studies and performed a log-transformed analysis of covariance to test for differences in time to 50% hatch between these two areas with incubation temperature as the covariate.

Results

Incubation rates

Temperatures of the three water baths increased at the beginning of sampling (Fig. 1). Temperature spikes that occurred after 288 hours in the 5.7°C jars and after 396 hours in the 3.8°C jars, were associated with the appearance of large numbers of larvae; water baths may have warmed when refrigerators were opened frequently to measure larvae.

Eggs developed at similar rates among incubation temperatures for the first 36 hours through stage 6 (Fig. 2). After stage 6, at about 36 hours, when temperatures had stabilized, development rates began to diverge. Duration of stages 7–21 was variable (Table 3). Usually the duration of a stage was longer at cooler temperatures. However, this was not always the case, and stages 12 and 20 required similar amounts of time regardless of temperature. At all temperatures, hatching began during stage 20; the percentage of eggs hatched by the beginning of stage 21 was 35% at 3.8°, 40% at 5.7°, and 8.1% at 7.7°C. Four larvae from the 7.7°C group hatched after 192 hours; another 18 hours elapsed before other larvae hatched at this temperature. These early larvae were not included in this analysis because we assumed that the hiatus in hatching times indicated that early hatching was anomalous, i.e. hatching may have been mechanically induced. After hatching began, time required for 50% hatch decreased as temperature increased: 48, 36, and 24 hours at 3.8°, 5.7°, and 7.7°C. The elapsed time between hatching of the first and last larvae was 72 hours at 3.8°C and 60 hours at both 5.7° and 7.7°C.

Eggs developed normally at 5.7° and 7.7°C; however, curvature of the spine was observed in some late-stage embryos incubated at 3.8°C. These abnormal eggs hatched, but most larvae were not measured because of curvature. Mean length at hatch of all larvae increased with incubation temperature: 4.15 (SD 0.380, n=100), 4.29 (SD 0.272, n=192), and 4.55 mm (SD 0.303, n=84) at 3.8°, 5.7°, and 7.7°C (Fig. 3). Mean lengths of larvae from the three temperature groups were significantly different ($P<0.05$). In addition, larval lengths increased as the hatching period progressed at all temperatures. Length of larvae hatching at stages 20 and 21 was significantly different at all temperatures ($P<0.01$); larvae that hatched at stage 21 were 9–13% longer than larvae that hatched at stage 20.

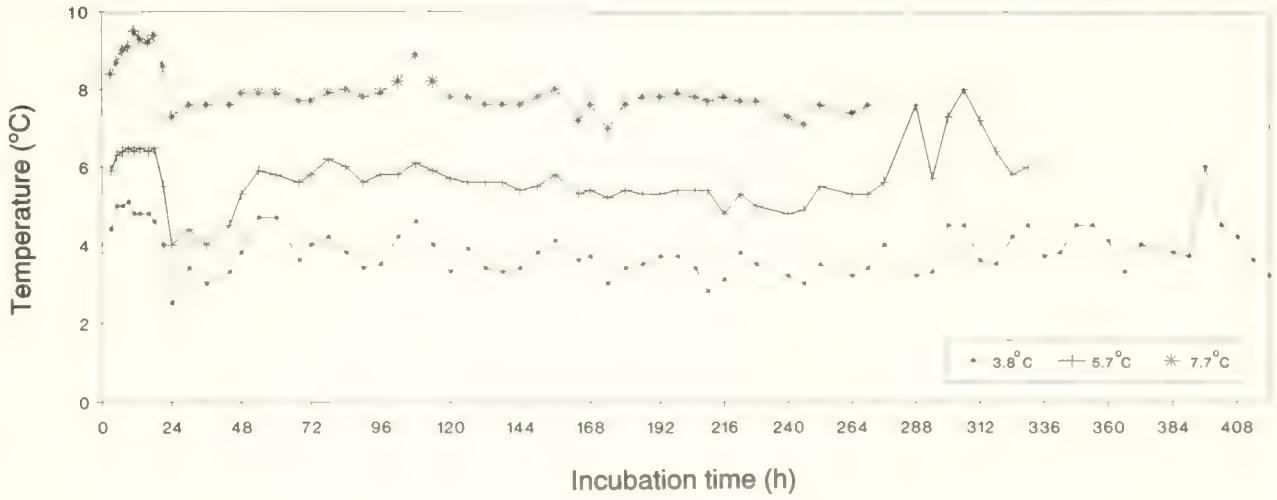

Figure 1

Temperatures recorded in water baths during incubation of *Theragra chalcogramma* eggs.

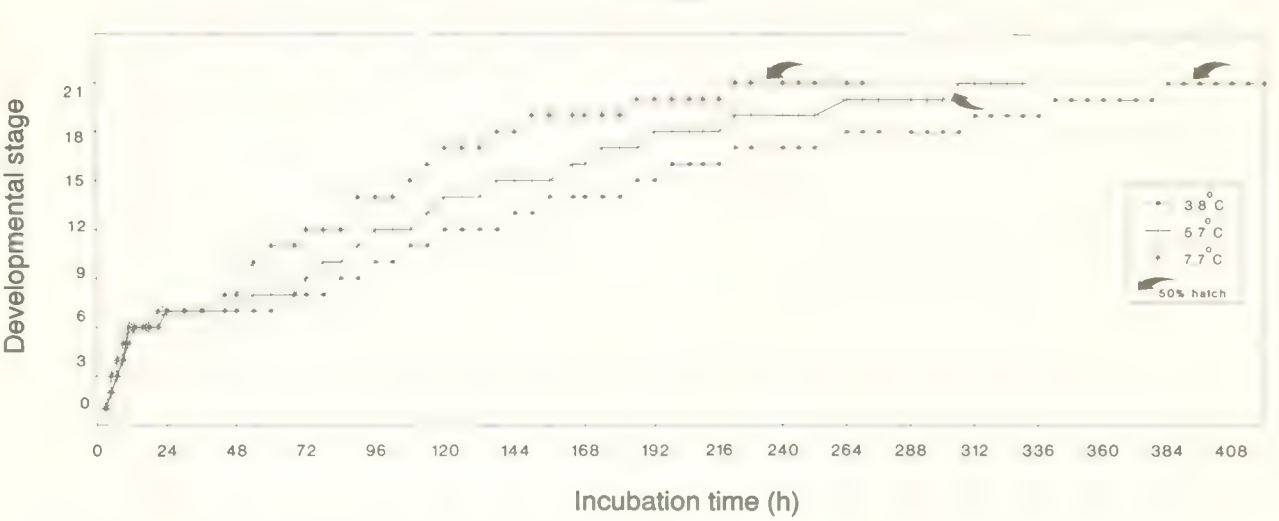

Figure 2

Development of *Theragra chalcogramma* eggs incubated at 3.8°, 5.7 , and 7.7 C. Points represent occurrence of stages at scheduled sampling times.

The piece-wise regression model (SAS, 1985) has two separate components and is discontinuous between stages 6 and 7 (Fig. 4). This type of model was necessary because of the rapid divergence of developmental rates at all temperatures after stage 6; it was not possible to fit one equation to the entire incubation time. The two components are described by the following equations:

component 1: stages 1–6

$$\text{Age} = 3.27 - 0.13\,(\text{stage})\,(\text{temperature}) + 0.47\,(\text{stage}^2);$$

component 2: stages 7–21

$$\text{Age} = 17.82 + 7.05(\text{stage}) - 0.656\,(\text{stage})\,(\text{temperature}) + 0.043(\text{stage}^3) - 0.0032\,(\text{temperature})\,(\text{stage}^3),$$

Table 3

Endpoint, midpoint, and duration in hours (h) of stage of development of *Theragra chalcogramma* eggs incubated at 3.8°, 5.7°, and 7.7°C.

	3.8°C			5.7°C			7.7°C		
Stage	Endpoint (h)	Midpoint (h)	Duration (h)	Endpoint (h)	Midpoint (h)	Duration (h)	Endpoint (h)	Midpoint (h)	Duration (h)
1	4.00	2.00	4.00	4.00	2.00	4.00	3.50	1.75	3.50
2	6.00	5.00	2.00	6.00	5.00	2.00	4.00	3.75	0.50
3	8.00	7.00	2.00	7.00	6.50	1.00	5.00	4.50	1.00
4	10.25	9.12	2.25	9.00	8.00	2.00	7.00	6.00	2.00
5	12.50	11.37	2.25	10.25	9.62	1.25	10.25	8.62	3.25
6	22.50	17.50	10.00	22.50	16.37	12.25	19.50	14.87	9.25
7	64.00	43.25	41.50	51.00	36.75	28.50	40.00	29.75	20.50
8	78.00	71.00	14.00	68.00	59.50	17.00	48.00	44.00	8.00
9	90.00	84.00	12.00	75.00	71.50	7.00	54.00	51.00	6.00
10	105.00	97.50	15.00	87.00	81.00	12.00	57.00	55.50	3.00
11	120.00	112.50	15.00	93.00	90.00	6.00	68.00	62.50	11.00
12	138.00	129.00	18.00	108.00	100.50	15.00	84.00	76.00	16.00
13	153.00	145.50	15.00	114.00	111.00	6.00	87.00	85.50	3.00
14	180.00	166.50	27.00	135.00	124.50	21.00	102.00	94.50	15.00
15	195.00	187.50	15.00	164.00	149.50	29.00	111.00	106.50	9.00
16	219.00	207.00	24.00	174.00	169.00	10.00	117.00	114.00	6.00
17	252.00	235.50	33.00	189.00	181.50	15.00	132.00	124.50	15.00
18	312.00	282.00	60.00	219.00	204.00	30.00	144.00	138.00	12.00
19	336.00	324.00	24.00	258.00	238.50	39.00	180.00	162.00	36.00
20	378.00	357.00	42.00	300.00	279.00	42.00	219.00	199.50	39.00
21	414.00	393.00[1]	36.00	330.00	303.00[1]	30.00	270.00	234.00[1]	51.00

[1] 50% hatch.

where age of the egg is expressed in hours. The value of R^2 is 0.96 for component 1 and 0.99 for component 2.

We compared our rates of egg development to other walleye pollock incubation studies in the 5–7°C range (Table 4). There was a significant difference between regression equations of incubation time to 50% hatch and temperature for western versus eastern North Pacific studies ($P<0.01$), but the slopes were not different ($P=0.18$). Based on the 95% confidence interval about the parameter estimates, time to 50% hatch of western North Pacific walleye pollock tended to be 1.2 to 1.3 times longer on average than that of the eastern North Pacific fish at a specific temperature.

Morphological descriptions

Walleye pollock eggs are pelagic and have a smooth, clear chorion and homogeneous yolk. No oil globules are present. Preserved eggs range from 1.2 to 1.8 mm in diameter, although most are 1.35–1.45 mm (Matarese et al., 1989). Appearance of the egg varies with type of preservative. There was little or no shrinkage of yolk material in Stockard's solution, whereas yolk of formalin-preserved eggs decreased in volume and the yolk membrane frequently collapsed. This effect of formalin preservation was helpful in determining how much of the tail had lifted away from the yolk in late-stage embryos.

Development of walleye pollock eggs and embryos, from fertilization to just before hatching, was divided into the following 21 stages (Table 2):

Precell (stage 1) Cytoplasm at the animal pole forms a blastodisc; bands of cytoplasm extend from below the equator to the blastodisc (Fig. 5A), which is without distinct margins (Fig. 6A). When intact, the yolk membrane almost touches the inner wall of the chorion. The perivitelline space is most visible over the blastodisc.

2 cells (stage 2) The first cell division of the blastodisc is in the horizontal plane. Cell material may not be equally divided (Figs. 5B and 6B).

4 cells (stage 3) The second cleavage is perpendicular to, and in the same plane as, the first. Cells are roughly equal in size and form a square (Figs. 5C and 6C).

8 cells (stage 4) The third cleavage is perpendicular to the second cleavage (parallel to first cleavage). Each cell divides in half in the horizontal

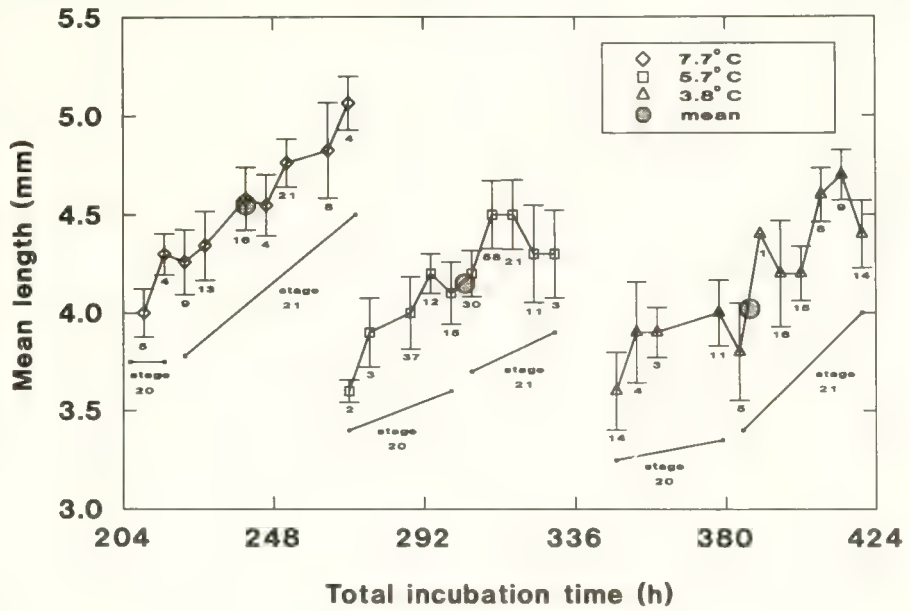

Figure 3

Mean hatch lengths at each sampling interval during the hatching period of *Theragra chalcogramma* larvae incubated at 3.8°, 5.7°, and 7.7°C. Stage of development at hatch is also shown. Shaded circle indicates overall mean length for each temperature. Vertical bars are standard deviations; numbers indicate sample size.

plane. Cells form a rectangle with the four cells in the center smaller than those at the corners of the rectangle (Figs. 5D and 6D).

16 cells (stage 5) The fourth cleavage is perpendicular to the third; this is the last stage in which cell division is restricted to the horizontal plane. Most eggs have a square or rectangular block of cells with four cells on each side; all cells are in contact with yolk through this stage (Figs. 5E and 6E).

32 cells (stage 6) Initially, the single layer of cells has a flat, irregular square or rectangular shape. Cell division continues in horizontal and vertical planes, transforming the blastodisc into a hollow cap of cells on the yolk resembling a raspberry (Figs. 5F and 6F). Cells increase in number but the size of the blastodisc remains constant. The perivitelline space widens between yolk and chorion.

Blastodermal cap (stage 7) The blastodisc progresses through two steps: at first, cell size decreases from continued cleavage; cell material appears granular and the blastodisc resembles a flattened dome on the yolk surface. Then, the base of the cell mass sinks below the yolk surface; the periblast extends beyond the equator of the blastodisc, giving the appearance of a "flying saucer" in lateral view (Figs. 5G and 6G).

Early germ ring (stage 8) The center of the blastodisc flattens and the periphery (germ ring) thickens in preparation to overgrow the yolk (epiboly). The blastocoel, visible on one side of the blastodisc, appears grainy and pale (Fig. 5H). The margin between blastocoel and blastodisc is indistinct (Fig. 6H).

Germ ring 1/4 around yolk (stage 9) The blastodisc, now the embryonic shield, expands as the germ ring begins to overgrow the yolk. The margin of the future anterior end of the embryo is slightly curved and sharply defined. Cell material covering the blastocoel appears less grainy than in the previous stage. After preservation, this thin cellular layer appears concave in lateral view. The germ ring margin is thin and flattened, extending 1/4 around yolk (Figs. 5I and 6I).

Germ ring 1/2 around yolk (stage 10) The germ ring envelopes half the yolk and the anterior margin of the embryonic shield is sharply curved and thick (Figs. 5J and 6J). The beginning of neural development is visible; a neural keel extends from the anterior margin of the embryonic shield to 2/3 its length (Fig. 5K).

Germ ring 3/4 around yolk (stage 11) Head and upper body region begin to differentiate but no distinct brain lobes are apparent. Optic vesicles develop. Prospective head and body mesoderm outlines the hour-glass shape of the developing embryo (Fig. 7A). The notochord is visible ventrally. The germ ring has progressed 3/4 down the yolk (Fig. 6K).

Late germ ring (stage 12) Myomere differentiation begins; separate myomeres are not visible. The midbody expands dorsoventrally; prospective head and body mesoderm forms a narrow outline of the embryo. The blastopore is open and the germ ring envelopes more than 7/8 of the yolk (Figs. 7B and 8A).

Early middle stage (stage 13) The blastopore is closed. The notochord and 7–12 incomplete myomeres are visible. Tail margin is indistinct and

flat; the medial portion of the tail bud is thicker (Figs. 7C and 8B). The body of the embryo appears flattened. Although not distinguishable in preserved specimens, Kupffer's vesicle is visible in the live egg.

Middle middle stage (stage 14) Embryos have 14–16 myomeres. Differentiation begins in eyes and mid- and hindbrain. Forebrain very small and underdeveloped. The tail bud margin is defined but still flattened (Fig. 8C). The entire length of the body is thicker. Small melanophores are scattered along the dorsum between the hindbrain and 4/5 of body length (Fig. 7D).

Late middle stage (stage 15) About 20–25 myomeres are visible. Eye lenses are formed. The liver appears as a slight bulge in the body wall, and the gut area is delineated. The tail bud is thick and appears lifted from the yolk surface with the margin attached (Fig. 7E). Pigment is darker than in the previous stage and dendritic, extending from midbrain to tip of tail bud and confined mostly to the dorsum. Nares, mid- and hindbrain, and pectoral bud anlagen are visible dorsally (Fig. 8D).

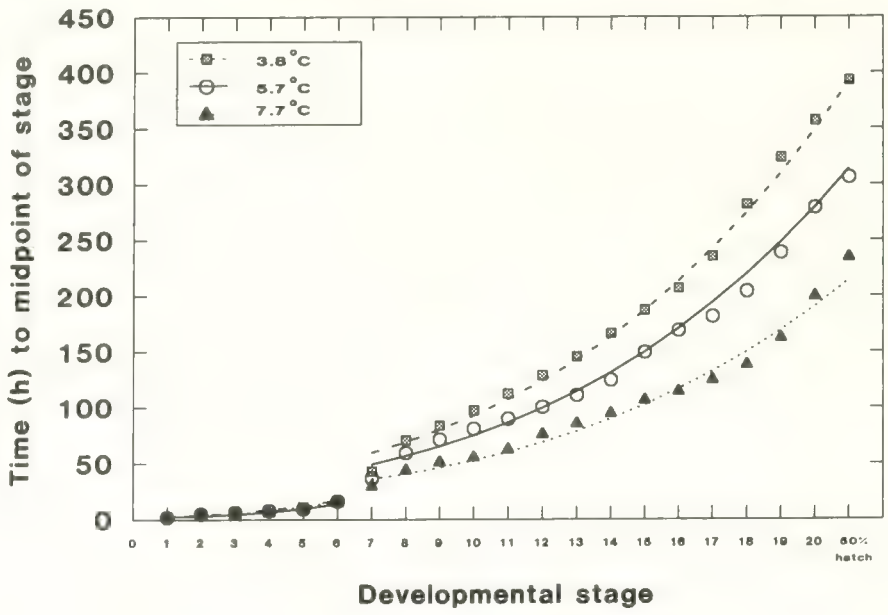

Figure 4

Time (h) to midpoint of stage of *Theragra chalcogramma* eggs incubated at 3.8°, 5.7°, and 7.7°C. Fitted lines are results of regression model; symbols are observed values.

Early late stage (stage 16) Heart tissue begins to expand when the embryo has about 24–36 myomeres. Forebrain differentiates from midbrain. The tail bud lifts from the yolk surface (Figs. 7F and 8E) and pigment forms two parallel rows dorsoposteriorly.

Tail 5/8 around yolk (stage 17) The embryo has 27–36 myomeres. More of the tail lifts from the

Table 4

Comparison of time (h) to estimated midpoint of five developmental milestones of *Theragra chalcogramma* embryos incubated at 5–7°C.

	Eastern North Pacific incubation studies				Western North Pacific incubation studies			
Stage	Matarese, 1983, unpubl.[1] (5.0°C)	Paul, 1984, unpubl.[2] (5.0°C)	Haynes and Ignell, 1983[3] (6.0°C)	This study (5.7°C)	Hamai et al., 1971[4] (6.5–6.7°C)	Yusa, 1954 (6.0–7.0°C)	Nakatani and Maeda, 1984[5] (7.0°C)	Hamai et al., 1974 (5.0°C)
Blastodermal cap	37.5	39.5	35	36.8		28.5	31	
Blastopore closure	114	118	105	108	100	102	148	139
Tail 3/4	211.7	217	161	204		234	192	
Tail full circle	274.5	264	250	279	250	270	216	330
50% hatch	349	320	285	303	345	288+	298	411

[1] A. C. Matarese, Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way N.E., Seattle, WA 98115.
[2] A. J. Paul, University of Alaska Fairbanks, Institue of Marine Science, Seward Marine Center Lab, P.O. Box 730, Seward, AK 99664. Values except for hatch estimated from Table 3 in Haynes and Ignell (1983). 50% hatch from Table 7.
[4] Values except for hatch estimated from Fig. 3 in Hamai et al. (1971).
[5] Values except for hatch estimated from Fig. 5 in Nakatani and Maeda (1984).

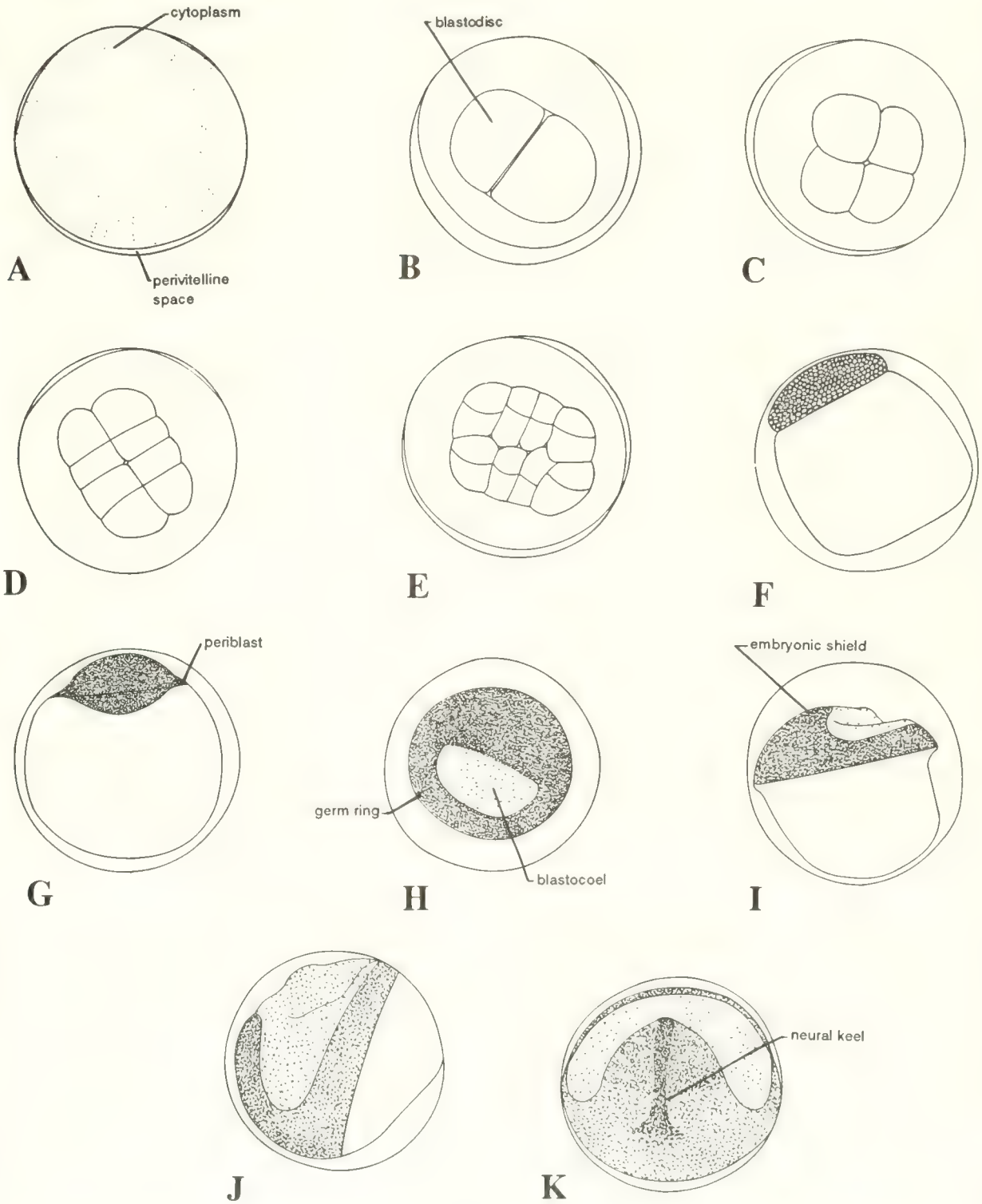

Figure 5

Illustrations of preserved *Theragra chalcogramma* eggs. (**A**) Stage 1 (precell); (**B**) Stage 2 (2 cell); (**C**) Stage 3 (4 cell); (**D**) Stage 4 (8 cell); (**E**) Stage 5 (16 cell); (**F**) Stage 6 (32 cell); (**G**) Stage 7 (blastodermal cap); (**H**) Stage 8 (early germ ring); (**I**) Stage 9 (germ ring 1/4, lateral view); (**J**) Stage 10 (germ ring 1/2, lateral view); (**K**) Stage 10 (dorsal view).

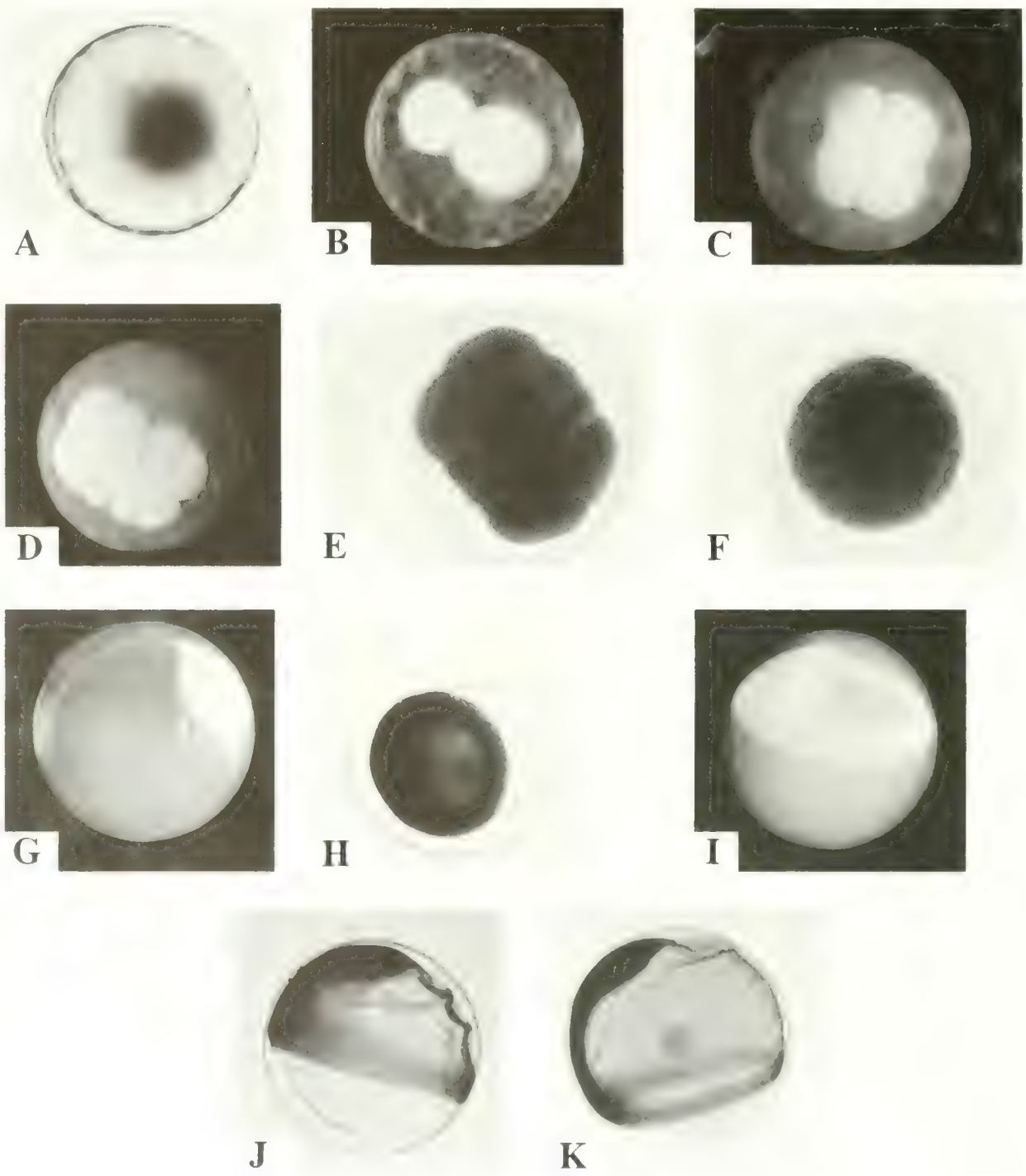

Figure 6

Photographs of preserved *Theragra chalcogramma* eggs. (**A**) Stage 1 (precell); (**B**) Stage 2 (2 cell); (**C**) Stage 3 (4 cell); (**D**) Stage 4 (8 cell); (**E**) Stage 5 (16 cell); (**F**) Stage 6 (32 cell); (**G**) Stage 7 (blastodermal cap); (**H**) Stage 8 (early germ ring); (**I**) Stage 9 (germ ring 1/4); (**J**) Stage 10 (germ ring 1/2); (**K**) Stage 11 (germ ring 3/4).

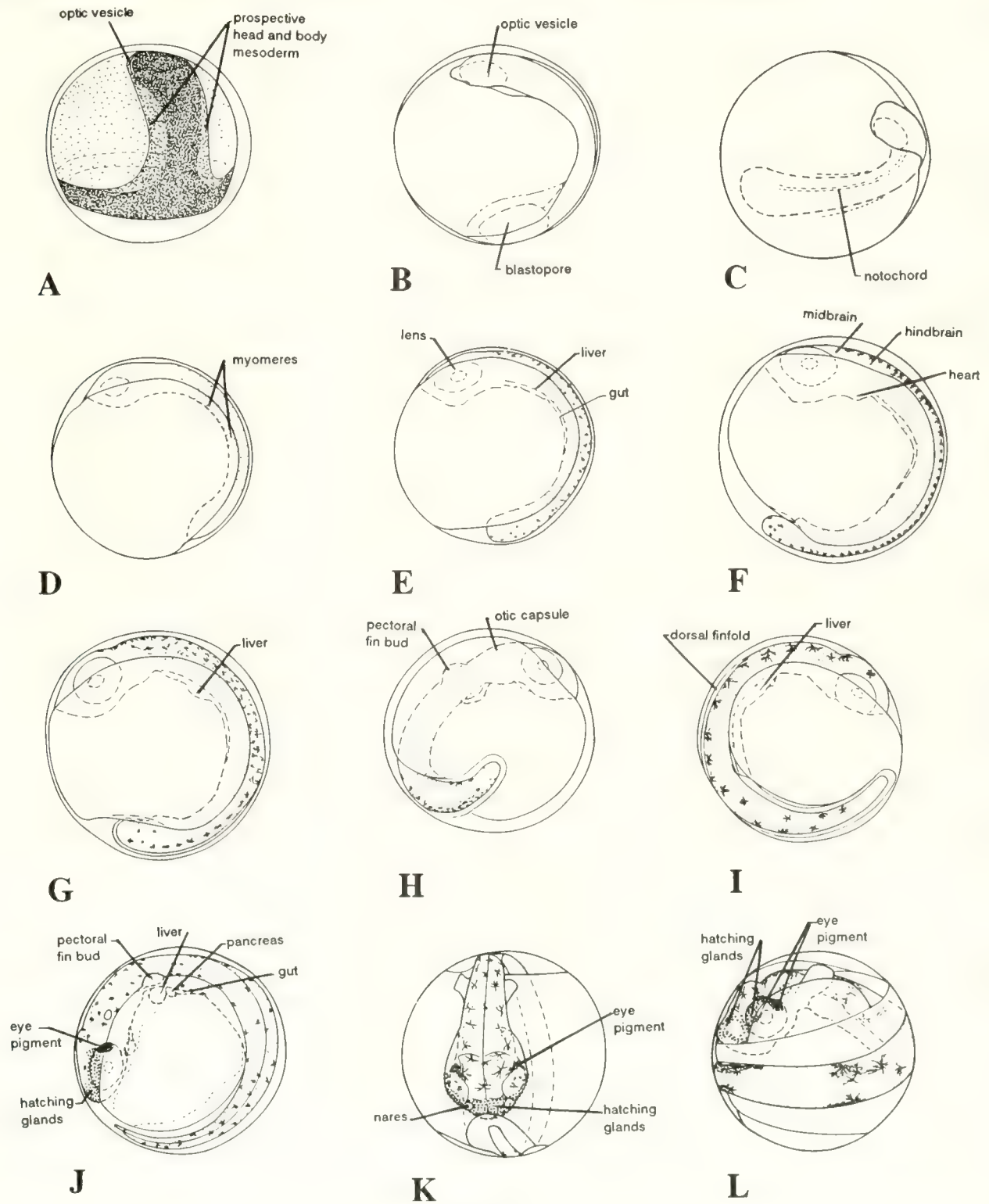

Figure 7

Illustrations of preserved *Theragra chalcogramma* eggs. (**A**) Stage 11 (germ ring 3/4); (**B**) Stage 12 (blastopore almost closed); (**C**) Stage 13 (early middle); (**D**) Stage 14 (middle middle); (**E**) Stage 15 (late middle); (**F**) Stage 16 (early late); (**G**) Stage 17 (tail 5/8 circle); (**H**) Stage 18 (tail 3/4 circle); (**I**) Stage 19 (tail 7/8 circle); (**J**) Stage 20 (tail full circle, lateral view); (**K**) Stage 20 (dorsal view); (**L**) Stage 21 (tail 1-1/8 circle).

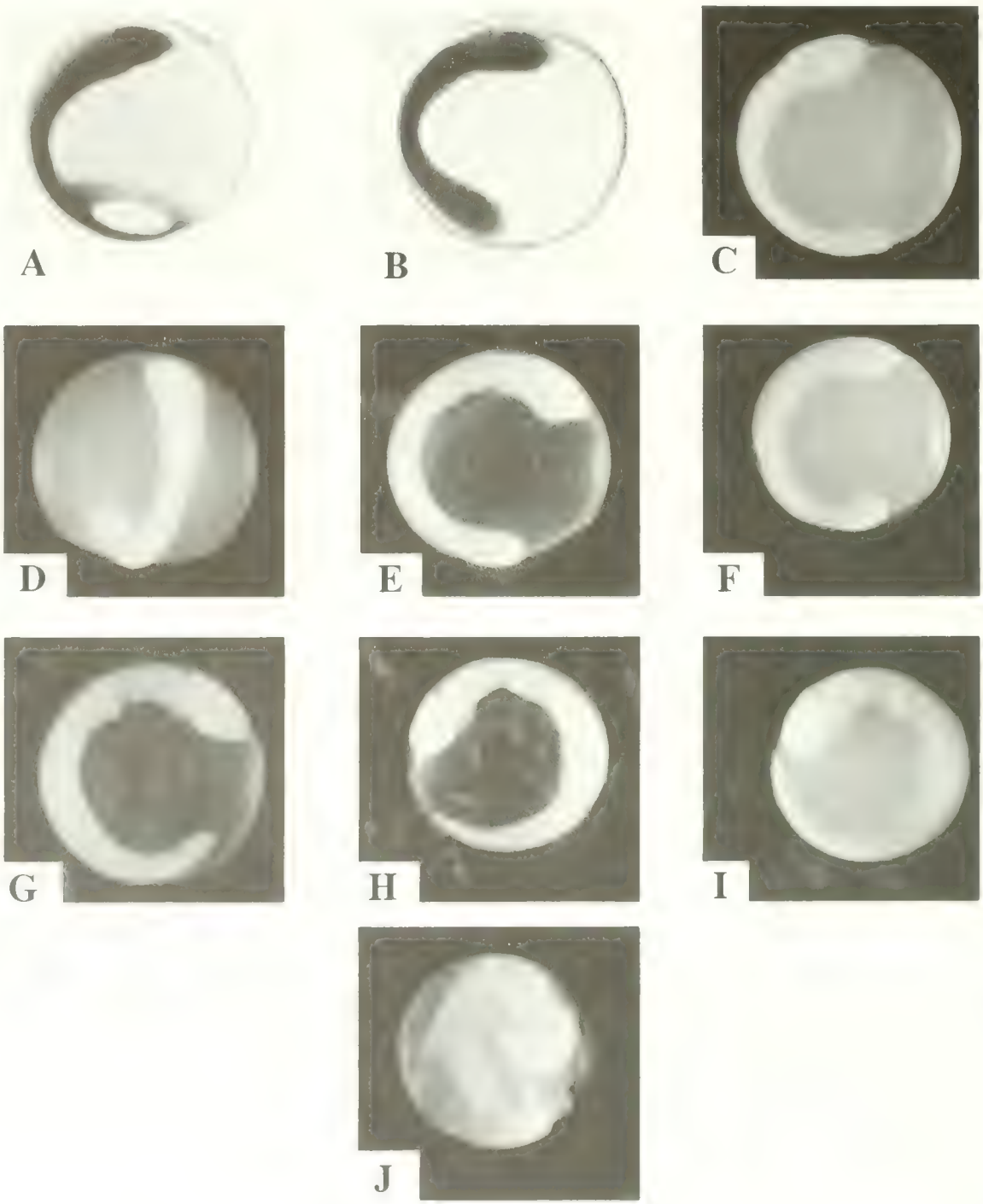

Figure 8

Photographs of preserved *Theragra chalcogramma* eggs. (**A**) Stage 12 (blastopore almost closed); (**B**) Stage 13 (early middle); (**C**) Stage 14 (middle middle); (**D**) Stage 15 (late middle); (**E**) Stage 16 (early late); (**F**) Stage 17 (tail 5/8 circle); (**G**) Stage 18 (tail 3/4 circle); (**H**) Stage 19 (tail 7/8 circle); (**I**) Stage 20 (tail full circle); (**J**) Stage 21 (tail 1-1/8 circle).

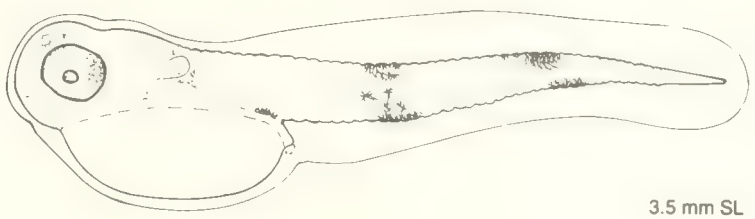

Figure 9
Illustration of preserved *Theragra chalcogramma* yolk-sac larva (Matarese et al., 1989).

yolk surface (Fig. 8F). The dorsal finfold is formed on the posterior 1/3 of the body and pigment on the head extends at least to the posterior margin of the eye (Fig. 7G). The liver is prominent and the heart is beating in the live egg.

Tail 3/4 around yolk (stage 18) The embryo has 36–41 myomeres. The tip of the tail is tapered and curves away from the longitudinal axis of the embryo (Fig. 7H). The dorsal finfold extends to midbody and pectoral fin buds are prominent. Otic capsules are formed. Large stellate melanophores are scattered over the dorsum, extending just to the midlateral surface; posterior to the anus, two rows of melanophores are seen dorsally and a few are found along the ventral midline (Fig. 8G). The tip of the tail is unpigmented.

Tail 7/8 around yolk (stage 19) When the embryo has 44–48 myomeres, the dorsal finfold extends anteriorly 2/3 body length, inserting just posterior to the pectoral fin buds and centered over the liver (Figs. 7I and 8H). Pigment on the head extends to the middle of the eye. At midbody, pigment is scattered on either side of the dorsal midline, extending to just above the lateral midline. Postanal pigment migrates toward the dorsal and ventral midlines.

Tail full circle around yolk (stage 20) The embryo has 48–49 myomeres and the pancreas is visible adjacent to the liver (Fig. 7J). The embryo now encircles the yolk and the tail tip may reach from near the snout to as far back as the posterior margin of the eye (Fig. 8I). Hatching glands, similar to those of other teleosts (Yamagami, 1988), are discernible on the surface of the snout and may extend over the dorsal surface of the eye (Figs. 7J and 7K). The posterior portion of the eye is pigmented. Postanal pigment migrates and begins to form the postanal bars found in yolk-sac larvae (Matarese et al., 1989) (Fig. 9).

Tail 1 1/8 times around yolk (stage 21) The embryo has 49–50 myomeres and the tail tip elongates, extending beyond the posterior margin of the eye (Fig. 8J). The urinary bladder is visible posterior to the anus (1/3 body length; not shown on figure) and the dorsal finfold extends to midbrain. Head pigment extends to the anterior margin of the eye (Fig. 7L). The dorsal half of the eye is pigmented. Most body pigment coalesces to three areas: dorsally, on gut; a bar at 1/2 body length; and a bar at 3/4 body length. In the postanal bars, most pigment is along dorsal and ventral midlines; some pigment extends onto the lateral body. Pigment is scattered on the preanal body.

Discussion

Time from first hatch to 50% hatch was inversely related to temperature. Hatch times reflected the effects of temperature described by Yamagami (1988), who demonstrated that the hatching enzyme secreted by the embryo solubilizes the chorion more rapidly at higher temperatures. The first larvae to hatch were stage 20. Early hatching may have been an artifact of rearing conditions. However, hatching glands were present at this stage, which, with the appearance of eye pigment, may correspond to a level of development that would enable these larvae to survive. Early hatching may occur naturally with some frequency. Within batches of walleye pollock larvae from Puget Sound that had been incubated in the laboratory, larvae hatching early grew to an equivalent size as larvae hatching later (larvae hatched on day 1 were the same length at day 3 as larvae hatched on day 3). Those early hatched larvae also began to feed at the same time as larvae hatched later.[4]

Rate of development and time to 50% hatch were similar among studies of walleye pollock from the eastern North Pacific, specifically the Gulf of Alaska (Matarese, unpubl. data; Haynes and Ignell, 1983; and this study; Paul[5]). From data on time (days) to 50% hatch for all temperatures reported in all incubation studies (Fig. 10), incubation times of western North Pacific walleye pollock are longer than eastern North Pacific walleye pollock.

This finding appears to conflict with Haynes and Ignell's (1983) comparison with Yusa's (1954) study in which they report similar rates of development

[4] Olla, B. Mark O. Hatfield Marine Science Center, Oregon State University, 2030 Marine Science Drive, Newport, OR 97365-5297. Pers. commun. 18 August 1992.

[5] Paul, A. J. University of Alaska Fairbanks, Institute of Marine Science, Seward Marine Center Lab, P.O. Box 730, Seward, AK 99664. Unpubl. data.

for eastern and western stocks. However, their comparison was made with midpoints of stages calculated from a regression model instead of observed midpoints. Also, Yusa (1954) reported a temperature range of 6–7°C instead of a mean; our interpretation of Haynes and Ignell's (1983) classification and calculation of Yusa's (1954) data suggests incubation temperatures were always above 6.5°C (see their Table 6 and our Table 4). Finally, Haynes and Ignell (1983) monitored midpoints of stages more closely than midpoint of hatch and did not specifically refer to 50% hatch.[6] We assumed the values reported as observed midpoints of hatch (their Table 7) were close to 50% hatch. Yusa's (1954) study could not be compared with ours with regard to time to 50% hatch.

Time of hatch is often a result of how eggs are treated during incubation and may vary with different batches.[7] However, walleye pollock eggs from Japanese waters are larger than those from the Gulf of Alaska (mean=1.4–1.6 mm and 1.3–1.4 mm, respectively; Bailey and Stehr, 1986). At similar temperatures, larger eggs take longer to develop (Pepin, 1991). The difference in incubation time emphasizes the need to collect data from fish specific to the area of interest. This will reduce the sources of variation in development time for laboratory-reared eggs; failure to identify and improve these sources would compromise the usefulness of models predicting egg age based on water temperature.

Development is a continuous process. The sampling intervals and arbitrary designation of stage endpoints break development into subjective units. Using the 21-stage scheme, we did not see a clear decrease in each stage duration with an increase in temperature. However, this will not affect the usefulness of our results. When stages are grouped to encompass a greater degree of morphological development, as in Haynes and Ignell (1983) and Picquelle and Megrey (1993), development time is inversely related to temperature. A greater number of stages within a group increases the accuracy of prediction of egg age. A large number of stages also allows others greater flexibility in grouping those stages.

Our regression model predicts temperature-specific development time for purposes of computing rates of egg production and egg mortality. There is no biological basis upon which the regression is predicated because stages that are assigned to the eggs are arbitrary; stages are ordinal data that are based on morphological criteria without consideration for development time. An alternative method to estimate development time from temperature is to fit a separate regression for each stage. The disadvantage of this alternative method is that many parameters are fitted with few data points.

Two studies describing morphological development, Gorbunova (1954) and Yusa (1954), have been published. Gorbunova (1954) was not comparable to our study. We compared our descriptions of morphological development with Yusa (1954). We assigned stages to descriptions of hourly morphological devel-

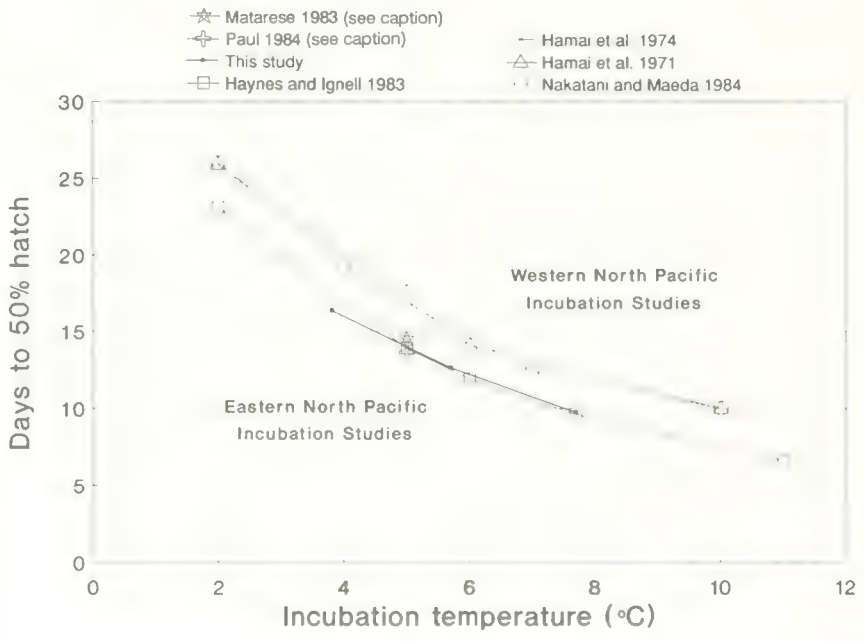

Figure 10

Days to 50% hatch for *Theragra chalcogramma* eggs at various temperatures of incubation. (A. C. Matarese, unpubl. data, Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way N.E., Seattle, WA 98115. A. J. Paul, unpubl. data, University of Alaska Fairbanks, Institute of Marine Science, Seward Marine Center Lab, P.O. Box 730, Seward, AK 99664.)

[6] Haynes, E., National Marine Fisheries Service, Auke Bay Laboratory, 11305 Glacier Highway, Juneau, AK 99801-8626. Pers. commun. April 1991.

[7] Paul, A. J., University of Alaska Fairbanks, Institute of Marine Science, Box 730, Seward, AK 99664. Pers. commun. 17 March 1992.

opment of walleye pollock embryos incubated at 6.0–7.0°C (Yusa, 1954) for comparison with morphological characteristics of eggs reared at 5.7°C in this study. We used hallmarks of each stage (e.g. number of cells, germ ring advancement, number of myomeres, tail growth around yolk) to distribute Yusa's (1954) descriptions into 21 stages. Yusa's (1954) descriptions were similar to ours up to stage 11. Beginning with stage 11, Yusa (1954) described the development of some structures occurring one or more stages earlier than this study: myomeres and nares were sighted one stage earlier; brain differentiation and eye lenses, two stages earlier; the heart, three stages earlier; and the otic capsules, five stages earlier (Table 5). Otoliths sighted by Yusa (1954) were not visible in our specimens. Conversely, eye pigment was observed in our study one stage earlier than that observed by Yusa (1954). Other structures appeared at the same stage in each study: optic vesicles, Kupffer's vesicle, liver, gut, and pectoral-fin anlagen. Also, after stage 13, similar numbers of myomeres were visible at like stages in both studies as was the beating of the heart.

Differences between the two studies may be the result of egg condition when examined: Yusa (1954) described live eggs, whereas most of our descriptions were of preserved eggs. Formalin preservation may obscure myomeres or destroy structures such as embryonic otoliths (McMahon and Tash, 1979). Stockard's solution darkens embryonic tissue and obscures fine details. Also, morphological development may differ between western and eastern North Pacific walleye pollock, further emphasizing the need to restrict data collection to specific areas of interest to increase accuracy of interpretation.

Acknowledgments

We thank the following people whose combined efforts helped us accomplish our research and produce this paper: William Rugen assisted with shipboard experiments; Kevin Bailey, Gail Theilacker, and Steve Porter helped us interpret the morphology of late-stage eggs and yolk-sac larvae; Trish Brown provided statistical analyses; Morgan Busby photographed the eggs; and Beverly Vinter illustrated eggs and helped interpret many morphological structures. We thank Art Kendall, A. J. Paul, Kevin Bailey, Susan Picquelle, and Bori Olla for preliminary reviews of the manuscript. Gail Theilacker and Richard Brodeur helped refine later versions. We also thank the members of FOCI who assisted with field collections.

Literature cited

Alderdice, D. F.
1988. Osmotic and ionic regulation in teleost eggs and larvae. *In* W. S. Hoar and D. J. Randall (eds.), Fish physiology, Vol. XI, Part A, p.163–251. Academic Press, Inc., San Diego.

Table 5

Descriptions of morphological development of *Theragra chalcogramma* embryos at comparable stages by Yusa (1954) and this study.

Stage	Yusa (6.0–7.0°C)	This study (5.7°C)
11	medullary plate and optic vesicles visible	optic vesicles visible
12	5–7 myomeres; 3 sections of brain visible	myomeres begin to differentiate
13	9–13 myomeres; heart, otic capsules, otoliths, eye lenses, and Kupffer's vesicle visible	7–12 myomeres; Kupffer's vesicle visible
14	16–17 myomeres; nares and pigment along dorsum visible	14–16 myomeres; pigment along dorsum visible; mid- and hindbrain differentiation
15	18–30 myomeres; liver, gut, and pectoral anlagen visible; 3 sections of brain formed	20–25 myomeres; eye lens, nares, pectoral anlagen, liver, and gut visible
16	35 myomeres	24–36 myomeres; heart visible; 3 sections of brain formed
17	37 myomeres; heart beating	27–36 myomeres; heart beating
18	40 myomeres	36–41 myomeres; otic capsules visible
19		44–48 myomeres
20		48–49 myomeres; eye pigment appears
21	eye pigment appears	

Bailey, K. M., and C. L. Stehr.
1986. Laboratory studies on the early life history of the walleye pollock, *Theragra chalcogramma* (Pallas). J. Exp. Mar. Biol. Ecol. 99:233–246.

Blaxter, J. H. S.
1969. Development: eggs and larvae. *In* W. S. Hoar and D. J. Randall (eds.), Fish physiology, Vol. III, p.177–252. Academic Press, New York.

Gorbunova, N. N.
1954. Reproduction and development of the walleye pollock, *Theragra chalcogramma* (Pallas). Tr. Inst. Okeanol. Akad. Nauk. SSSR 11:132–195. (In Russian, transl. by S. Pearson, 1972, Natl. Mar. Mammal Lab., NMFS, 7600 Sand Point Way N.E., Seattle, WA 98115–0070.)

Hamai, I., K. Kyushin, and T. Kinoshita.
1971. Effect of temperature on the body form and mortality in the development and early larval stages of the Alaska pollock, *Theragra chalcogramma* (Pallas). Bull. Fac. Fish. Hokkaido Univ. 22:11–29.

Hamai, I., K. Kyushin, and T. Kinoshita.
1974. On the early larval growth, survival, and variation of body form in the walleye pollock, *Theragra chalcogramma* (Pallas), in rearing experiment feeding the different diets. Bull. Fac. Fish. Hokkaido Univ. 25:20–35.

Haynes, E. B., and S. E. Ignell.
1983. Effect of temperature on rate of embryonic development of walleye pollock, *Theragra chalcogramma*. Fish. Bull. 81:890–894.

Kendall, A. W., Jr., and S. Kim.
1989. Buoyancy of walleye pollock (*Theragra chalcogramma*) eggs in relation to water properties and movement in Shelikof Strait, Gulf of Alaska. *In* R. J. Beamish and G. A. McFarlane (eds.), Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, p.169–180. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Kendall, A. W., Jr., and S. J. Picquelle.
1990. Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Fish. Bull. 88:133–154.

Markle, D. F., and K. G. Waiwood.
1985. Fertilization failure in gadids: aspects of its measurement. J. Northw. Atl. Fish. Sci. 6:87–93.

Matarese, A. C., A. W. Kendall Jr., D. M. Blood, and B. M. Vinter.
1989. Laboratory guide to early life history stages of Northeast Pacific fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 80, 652 p.

McMahon, T. E., and J. C. Tash.
1979. Effects of formalin (buffered and unbuffered) and hydrochloric acid on fish otoliths. Copeia 1979:155–156.

Megrey, B. A.
1991. Population dynamics and management of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska, 1976–1986. Fish. Res. 11:321–354.

Nakatani, T., and T. Maeda.
1984. Thermal effect on the development of walleye pollock eggs and their upward speed to the surface. Bull. Jpn. Soc. Sci. Fish. 50:937–942.

Naplin, N. A., and C. L. Obenchain.
1980. A description of eggs and larvae of the snake eel, *Pisodonophis cruentifer* (Ophichthidae). Bull. Mar. Sci. 30:413–423.

Olla, B. L., and M. W. Davis.
1993. The influence of light on egg buoyancy and hatching rate of the walleye pollock, *Theragra chalcogramma* (Pallas). J. Fish. Biol. 42:693–698.

Pepin, P.
1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. 48:503–518.

Picquelle, S. J., and B. A. Megrey.
1993. A preliminary spawning biomass estimate of walleye pollock, *Theragra chalcogramma,* in the Shelikof Strait, Alaska, based on the annual egg production method. Bull. Mar. Sci. 53:728–749.

Reed, R. K., and J. D. Schumacher.
1989. Transport and physical properties in central Shelikof Strait, Alaska. Cont. Shelf Res. 9:261–268.

SAS Institute, Inc.
1985. SAS® user's guide: basics, version-5 edition. SAS Institute, Inc., Cary, NC, 1290 p.

Schumacher, J. D., and A. W. Kendall Jr.
1991. Some interactions between young walleye pollock and their environment in the western Gulf of Alaska. Calif. Coop. Oceanic Fish. Invest. Rep. 32:22–40.

Trinkaus, J. P.
1951. A study of the mechanism of epiboly in the egg of *Fundulus heteroclitus*. J. Exp. Zool. 118:269–319.

Velsen, F. P. J.
1980. Embryonic development in eggs of sockeye salmon, *Oncorhynchus nerka*. Can. Spec. Pub. Fish. Aquat. Sci. 49, 19 p.

Yamagami, K.
1988. Mechanisms of hatching in fish. *In* W. S. Hoar and D. J. Randall (eds.), Fish physiology, Vol. XI, Part A, p. 447–499. Academic Press, Inc., San Diego.

Yusa, T.
1954. On the normal development of the fish, *Theragra chalcogramma* (Pallas), Alaska pollock. Bull. Hokkaido Reg. Fish. Res. Lab. 10:1–15.

Diel vertical distribution of ichthyoplankton in the northern Gulf of Alaska*

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Abstract.—The diel vertical distribution patterns of several abundant ichthyoplankton taxa were examined from depth-stratified tows off Kodiak Island in the western Gulf of Alaska during 1986 and 1987. Most larvae were found in the upper 45 m of the water column throughout the diel period but were concentrated in higher densities near the surface (0–15 m) in daylight hours and at greater depths at night. Four of the five dominant taxa examined in detail showed significantly greater weighted mean depths during the night than during the day. This pattern was the opposite to that previously reported for the numerically dominant taxa (*Theragra chalcogramma*) in this area. Since there was no clear relation between the diel vertical distribution of these taxa and the vertical distribution of water temperature and density or copepod nauplii prey, we hypothesize that this reverse migration is either a strategy to minimize spatial overlap with predators that follow a normal diel migration pattern or one to optimize light levels for feeding.

Planktonic eggs and larvae of marine fishes exist in three dimensions in the open ocean. Unfortunately, traditional ichthyoplankton surveys, which use non-closing sampling gear, provide information only on two dimensions, integrating the vertical indirectly into the horizontal dimensions. It is well known that vertical current shear can be substantial over short distances and that light, temperature, hydrostatic pressure and food show much stronger gradients in the vertical relative to the horizontal dimensions in the water column (Laprise and Dodson, 1993). Thus, a larva can often change not only its geographic position, but also its immediate environment by altering its vertical position in the water column.

Diel vertical migration is well documented for larval, juvenile, and adult life history stages of marine fishes (see review by Neilson and Perry, 1990). The adaptive significance of these migrations is presently in dispute, but it has been attributed to position maintenance, bioenergetic optimization, thermoregulation, and predator avoidance (Kerfoot, 1985; Lampert, 1989). In addition, the degree of migration and amplitude of depths over which a species vertically migrates often changes during ontogenetic development (Brewer and Kleppel, 1986; de Lafontaine and Gascon, 1989).

Knowledge of vertical distribution patterns of marine fish larvae is crucial not only in understanding ecological processes but also has practical implications in the assessment of abundance. Sampling just the upper depths of a species range can lead to substantial underestimates of abundance, whereas sampling the entire water column for surface-dwelling taxa may waste limited ship time. Despite the importance of the larval phase in recruitment of marine fishes, relatively little is known about larval vertical distribution patterns off the continental shelf in the North Pacific Ocean. With the exception of walleye pollock, *Theragra chalcogramma*, which has been fairly well studied through much of its geographic range (Kamba, 1977; Kendall et al., 1987; Pritchett and Haldorson, 1989; Kendall et al.[1]), the only comprehensive studies on vertical distribution of coastal ichthyoplankton in the northeast Pacific Ocean are from the California Current region (Ahlstrom, 1959; Boehlert et al., 1985; Brewer and Kleppel, 1986; Lenarz et al., 1991). This paper presents information on the vertical distribution of five abundant ichthyoplankton taxa (other than walleye pollock) collected in the

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coastal waters of Alaska during spring and examines diel differences in these patterns in relation to environmental and biotic factors.

Materials and methods

Samples examined were collected from two cruises of the NOAA ship *Miller Freeman* in the area southwest of Kodiak Island in the northern Gulf of Alaska (Fig. 1). During May 1986 and 1987, 22 depth-stratified tows were made with a 1-m^2 Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) (Wiebe et al., 1976) equipped with 153-µm mesh. The net was towed obliquely and nets were opened sequentially at the desired depth strata. The primary purpose of the sampling was to collect information on the vertical distribution of walleye pollock larvae, which are generally found in the upper 50 m (Kendall et al.[1]), and their prey. Therefore, the emphasis during the sampling was on the upper part of the water column. The nets sampled the following nominal depths: 0–15, 15–30, 30–45, 45–60, 60–80, 80–100, and >100 m. Maximum sampling depth varied (range 150–252 m) depending on the depth of the water column at a particular station. There were eight depth strata sampled at most stations but the cutoff depth between the seventh and eighth net was variable. Therefore, we pooled the catches from these two nets into a single depth stratum (>100 m) for analysis. The actual sampling depths are given in Table 1. More complete station and catch information is given in Siefert et al.[2,3]

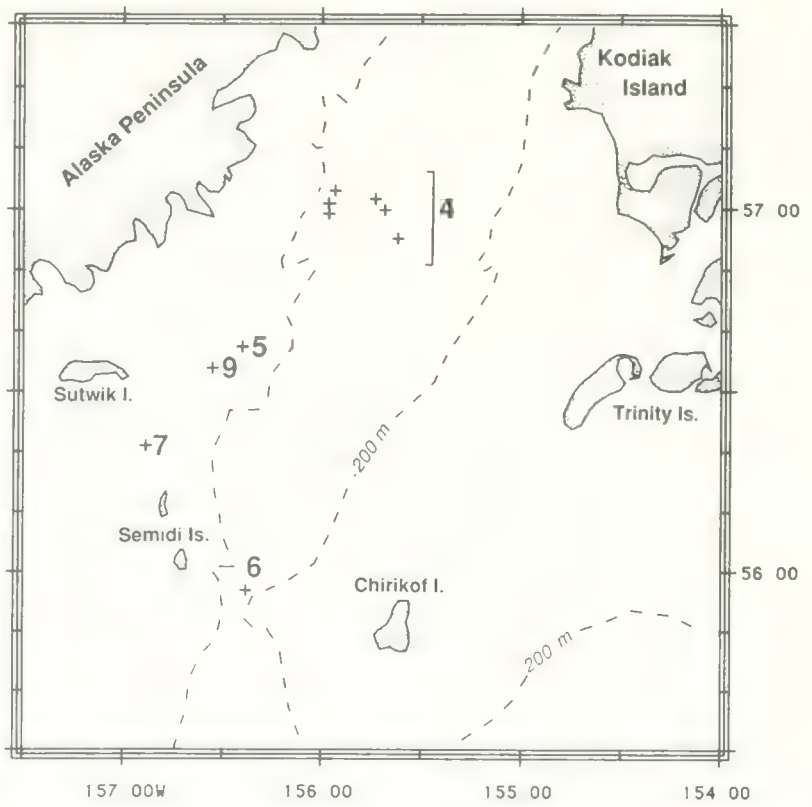

Figure 1

Location of MOCNESS sampling series in Shelikof Strait used to determine vertical distribution of larvae in 1986 and 1987.

The 22 tows were grouped into five collection series (Table 1) based upon date and location of sampling (see Kendall et al.[1]) and included two complete diel series. The first diel series (Series 4) attempted to sample the same body of water over a four day period during 1986 by following a radar-tracked drifter drogued at 35 m (Incze et al., 1990). The second diel series (Series 9) sampled the same location on three successive days during 1987. Other collections (Series 5, 6, and 7) were taken at various times of the day but in the same general area as these two series (Fig. 1, Table 1).

Retrieved nets were thoroughly washed and contents were preserved in 5% buffered formalin. Samples were sorted to the lowest possible taxon and life history stage at the Polish Sorting Center in Szczecin, Poland. The volume filtered was estimated from a mechanical flowmeter mounted on the MOCNESS frame and abundances were converted to number per 1000 m^3. Up to 50 preserved larvae of each taxon from each net were measured to the nearest 0.1 mm standard length. Net depth, temperature, and

[1] Kendall, A. W., Jr., L. S. Incze, P. B. Ortner, S. R. Cummings, and P. K. Brown. In review. The vertical distribution of eggs and larvae of walleye pollock (*Theragra chalcogramma*) in Shelikof Strait, Gulf of Alaska. Submitted to Fish. Bull.

[2] Siefert, D. L. W., L. S. Incze, and P. B. Ortner. 1988. Vertical distribution of zooplankton, including ichthyoplankton, in Shelikof Strait, Alaska: data from Fisheries Oceanography Coordinated Investigations (FOCI) cruise in May 1986. NWAFC Processed Rep. 88-28, 232 p.

[3] Siefert, D. L. W., L. S. Incze, and P. B. Ortner. 1990. Vertical distribution of zooplankton, including ichthyoplankton, in Shelikof Strait, Alaska: data from Fisheries Oceanography Coordinated Investigations (FOCI) cruise in May 1987. NWAFC Processed Rep. 90-05, 129 p.

Table 1

Station and tow data for collection subset used in the diel series ordered by time of day.

Series	Tow	Year	Date	Bottom depth (m)	Local time	Time period	Net depths (m) 1	2	3	4	5	6	7
4	5	1986	10 May	293	0745	Dawn	2–15	15–30	29–45	46–58	59–78	79–99	101–229
4	1	1986	8 May	220	0746	Dawn	1–15	15–31	35–45	45–61	61–80	80–100	101–200
9	4	1987	23 May	201	0747	Dawn	0–15	15–30	30–45	45–60	60–80	80–100	100–150
9	8	1987	24 May	190	0800	Dawn	0–15	15–30	30–45	45–60	60–80	80–100	100–150
6	2	1986	15 May	223	0940	Day	2–14	15–29	30–44	45–60	61–80	80–100	100–175
5	1	1986	13 May	210	1010	Day	2–15	16–30	30–45	45–61	61–80	80–100	101–152
4	6	1986	10 May	296	1341	Day	2–14		30–45			77–99	99–214
5	2	1986	13 May	210	1351	Day	2–14	15–29	30–44	45–59	59–78	80–99	100–176
4	2	1986	8 May	227	1356	Day	2–14	15–30	30–47			79–99	99–200
9	5	1987	23 May	179	1422	Day	0–15	15–30	30–45	45–60	60–80	80–100	100–150
9	9	1987	24 May	190	1543	Day	0–15	15–30	30–45	45–60	60–80	80–100	100–150
7	2	1986	18 May	123	1911	Dusk	2–15	15–30	30–45	45–59	60–79	80–100	
4	3	1986	9 May	235	2006	Dusk	2–13	13–28	29–45	46–59	60–79		100–200
4	7	1986	11 May	293	2011	Dusk	3–14	14–30	31–44	43–59	60–78	78–97	98–252
9	6	1987	24 May	179	2107	Dusk	0–15	15–30	30–45	45–60	60–80	80–100	100–150
9	10	1987	25 May	196	2122	Dusk	0–15	15–30	30–45	45–60	60–80	80–100	100–150
5	3	1986	14 May	210	2200	Night	2–14	14–30	30–45	46–60	60–80	81–101	100–163
7	1	1986	17 May	126	2416	Night	1–15	16–30	31–45	45–59	60–80	80–99	
4	4	1986	9 May	242	0135	Night	2–15	15–30	30–58		59–80	80–100	100–202
9	11	1987	25 May	198	0218	Night	0–15	15–30	30–45	45–60	60–80	80–100	100–150
9	7	1987	24 May	195	0219	Night	0–15	15–30	30–45	45–60	60–80	80–100	100–150
6	1	1986	15 May	229	0353	Night	2–15	15–29	30–44	45–60	60–80	80–100	100–172

salinity were measured continuously in real time during the tow and stored for later analysis.

To examine diel variations in density and size of larvae with depth, collections from the 22 tows were grouped into one of four time periods (hours): dawn (0530–0830), day (0830–1830), dusk (1830–2130), and night (2130–0530). Diel-depth variation in density of eggs and larvae at each depth was examined by using a two-way ANOVA on log-transformed data. The log $(X+1)$ transformation was used to achieve homogeneous variances (Bartlett's Test, all $P>0.05$). In addition, a weighted mean depth of occurrence of eggs or larvae of the dominant species for each time interval was calculated as follows:

$$\overline{D}_t = \frac{\sum_{i=1}^{n_t}\sum_{j=1}^{7} N_{ijt} D_{ijt}}{\sum_{i=1}^{n_t}\sum_{j=1}^{7} N_{ijt}},$$

where n_t = number of tows in time interval t,
N_{ijt} = number of larvae in net j in tow i in time interval t,
D_{ijt} = midpoint depth of net j in tow i in time interval t with a variance equal to

$$Var(\overline{D}_t) = \frac{n_t}{\left(\sum_{i=1}^{n_t} N_{it}\right)^2 (n_t - 1)} \sum_{i=1}^{n_t} N_{it}^2 (\overline{D}_{it} - \overline{D}_t)^2,$$

where N_{it} = number of larvae in tow i in time interval t.

Differences in the weighted mean depths over the four time periods were tested with ANOVA, and Tukey multiple-comparison tests were conducted when significant differences were observed. Untransformed larval lengths for the three most abundant species were entered as dependent variables in two-way ANOVAs, with time of day and depth as factors.

Results

Species composition

Eggs and larvae of species other than walleye pollock were found in 134 of the 145 samples collected

during the 1986 and 1987 cruises. Flathead sole (*Hippoglossoides elassodon*) eggs were the only pelagic eggs other than walleye pollock collected and were found in 28.4% of the samples. This species had a mean density of 62.99 eggs/1000 m^3 (SD=179.66) and comprised 74.9% of the total egg abundance in the 22 tows.

A total of 33 larval taxa were identified but only a few taxa occurred in more than 10% of the samples (Table 2). Larvae other than walleye pollock occurred in 92.4% of the collections but made up only 26.3% of the overall total abundance of larvae (total mean density=143.61 larvae/1000 m^3; SD=257.03). Larvae of three taxa (*H. elassodon*, *Ammodytes hexapterus*, and *Bathymaster* spp.[4]) were found at sufficient densities to enable examination of their vertical abundance and length distribution patterns in detail for the four time periods. Two other species (*Gadus macrocephalus* and *Pleuronectes bilineatus*) were found at relatively high densities during day and night but at low densities during the twilight periods; hence, these taxa were examined only for day-night differences.

Vertical distribution

The distribution of *H. elassodon* eggs showed little variation in weighted mean depth by time of day (F=3.10, P>0.05); the highest abundances were

[4] Larvae of three *Bathymaster* species known to occur in the study area are presently not identifiable to species. Based on the abundance and distribution patterns of the adults, most of the larvae present in our collections are probably *B. signatus*. (A. Matarese, Alaska Fisheries Science Center, Seattle, WA 98115. Pers. commun. 1992).

Table 2

Summary of all larvae including walleye pollock collected in the 1986–87 vertical distribution study.

Scientific name	Common name	Percent occurrence (n=145)	Mean density (no./1000m^3)	Length range (mm)
Osmerus mordax	rainbow smelt	0.69	0.25	21
Leuroglossus schmidti	northern smoothtongue	0.69	0.02	9–15
Stenobrachius leucopsarus	northern lampfish	4.14	3.05	4–7
Protomyctophum thompsoni	bigeye lanternfish	0.69	0.04	10
Myctophidae	unidentified myctophid	0.69	0.06	3
Gadus macrocephalus	Pacific cod	15.86	27.51	3–11
Theragra chalcogramma	walleye pollock	93.79	402.71	3–8
Gadidae	unidentified gadid	2.76	0.36	4
Sebastes spp.	unidentified rockfish	1.38	0.17	4–5
Hexagrammos decagrammus	kelp greenling	1.38	0.05	8–11
Dasycottus setiger	spinyhead sculpin	0.69	0.07	8
Gymnocanthus spp.	unidentified sculpin	0.69	0.07	7–8
Hemilepidotus hemilepidotus	red Irish lord	1.38	0.13	11–13
Icelinus spp.	unidentified sculpin	7.59	0.65	4–5
Malacocottus zonurus	darkfin sculpin	0.69	0.05	6–7
Radulinus asprellus	slim sculpin	1.38	0.10	4–5
Ruscarius meanyi	Puget Sound sculpin	0.69	0.04	4
Agonidae	unidentified poacher	10.34	0.84	5–10
Nectoliparis pelagicus	tadpole sculpin	0.69	0.07	4–8
Cyclopteridae	unidentified snailfish	2.07	0.19	4–5
Bathymaster spp.	unidentified ronquil	13.10	30.67	4–7
Anoplarchus spp.	unidentified prickleback	2.07	0.26	8–10
Lumpenella longirostris	longsnout prickleback	1.38	0.05	10–11
Lumpenus maculatus	daubed shanny	6.21	0.64	12–23
Poroclinus rothrocki	whitebarred prickleback	4.83	0.97	10–15
Cryptacanthodes aleutensis	dwarf wrymouth	1.38	0.19	14
Pholis spp.	unidentified gunnel	0.69	0.04	13–17
Zaprora silenus	prowfish	3.45	0.40	12–14
Ammodytes hexapterus	Pacific sand lance	40.69	12.76	6–19
Hippoglossoides elassodon	flathead sole	17.93	59.81	4–19
Pleuronectes bilineatus	rock sole	13.10	3.71	3–10
Pleuronectes vetulus	English sole	0.69	0.13	8
Psettichthys melanostictus	sand sole	0.69	0.14	4–5
Pleuronectidae	unidentified flounder	0.69	0.10	4

found in the surface layer (0–15 m) during all four time periods (Fig. 2). Although there were significant (P=0.005) differences in density by depth strata, neither the diel density differences alone (P=0.838) nor the interaction between time and depth (P=0.996) was significant.

The majority of larvae, excluding pollock larvae, from all collections combined were collected from the upper three depth strata (Fig. 3). The maximum density overall occurred at the second depth stratum (15–30 m), below which larval density declined with depth. However, this overall vertical distribution pattern was apparently confounded by higher larval densities found during the night when the larvae were mainly caught in the 15–30 m stratum; during the other three time periods the highest densities were in surface waters (Fig. 4). The weighted mean depth of larvae overall was significantly (P<0.05) greater at night than during the other three time periods (Table 3) and the interaction between time and depth was marginally significant (P=0.05; Table 4), suggesting that there were diel differences in overall larval depth distribution.

Four of the five most abundant larval taxa showed the greatest weighted mean depths (Table 3) and the lowest surface densities (Fig. 4) at night. This general pattern was also evident in the two time periods examined for the fifth species, *G. macrocephalus*, but the diel differences were not significant (Table 3). Only *A. hexapterus* and *G. macrocephalus* showed significant diel differences in larval density, with highest densities occurring at night (Table 4). None of the dominant taxa, however, showed a significant interaction between time and depth strata.

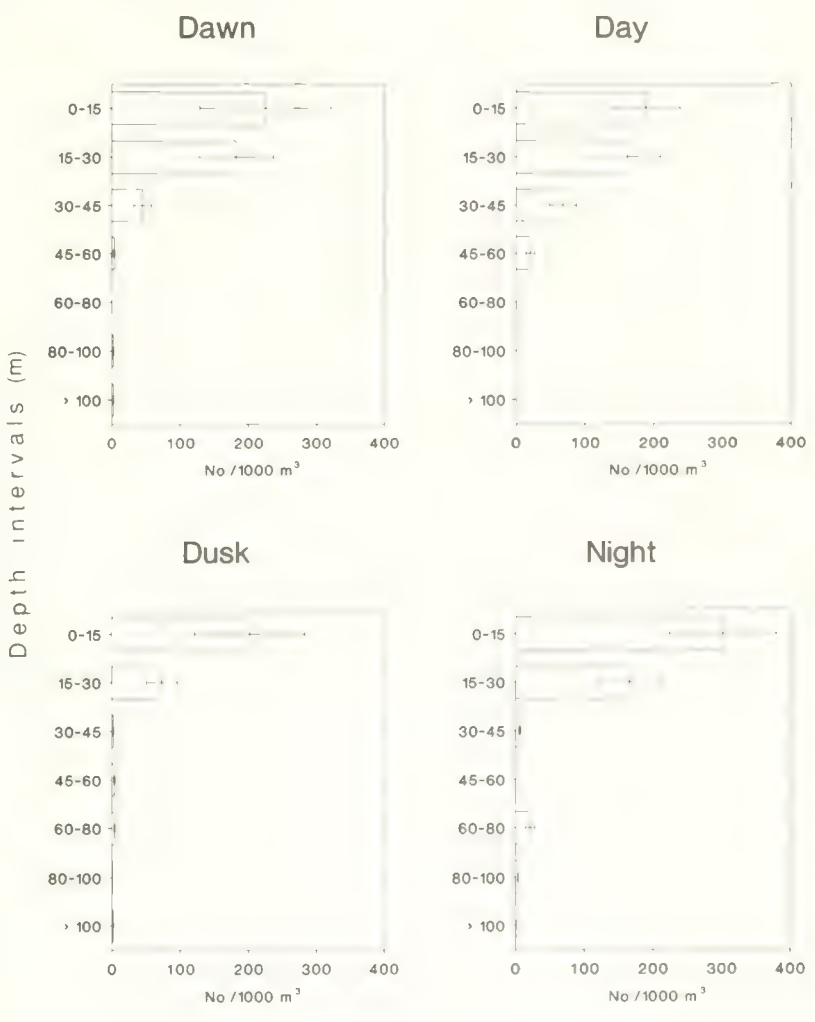

Figure 2

Diel vertical distribution of *Hippoglossoides elassodon* eggs. Bars are mean abundances per 1000 m^3 at each depth interval and error bars are ± one standard deviation about the mean abundance.

Length distributions

The distribution of larval lengths by time of day and depth showed no consistent pattern among the three most abundant species (Fig. 5). Although time and time-depth interactions were significant (all P<0.03) factors in explaining the variation in mean length of *H. elassodon* and *Bathymaster* spp., none of the factors was significant for *A. hexapterus*. Examining only the strata where more than two lengths were available, we found that the smallest larvae of both *Bathymaster* spp. and *A. hexapterus* were caught in the surface stratum at night but in deeper strata during daylight hours (Fig. 5). However, *H. elassodon* showed an increase in mean length with depth during daylight hours and the reverse pattern at night (Fig. 5). *Hippoglossoides elassodon* was the only taxon to show a significant difference in length distributions between night and day collections (Kolmogorov-Smirnov Test; Z=3.881; P=0.001). Although the lack of larger larvae in daytime collections might suggest some daytime gear avoidance by this species

(Fig. 6), there were few small larvae caught at night, which cannot be explained by gear avoidance. Since the majority (>95%) of these lengths were from larvae collected from the same location (Series 9), sampling variability cannot be invoked as an explanation for this pattern.

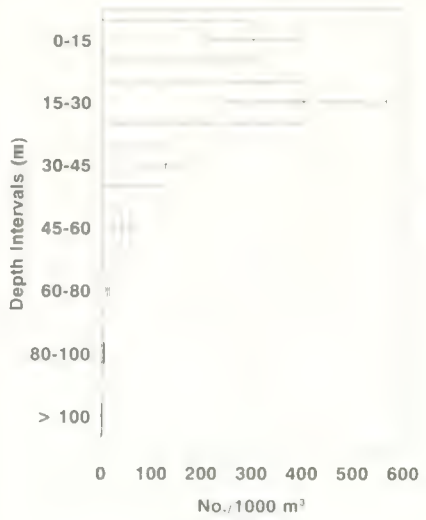

Figure 3

Vertical distribution of all larvae excluding walleye pollock (*Theragra chalcogramma*) combined over all time periods. Bars are mean abundances per 1000 m^3 at each depth interval and error bars are ± one standard deviation about the mean abundance.

Discussion

Our results indicate that the vast majority (>99%) of pelagic eggs and larvae (excluding walleye pollock) are distributed in the upper 100 m of the water column during the spring months. Therefore, sampling to this depth should be sufficient to characterize the horizontal distribution patterns of these species. Of the common taxa we examined, all but *H. elassodon* have demersal eggs (Matarese et al., 1989). The transit time to surface waters following hatching from demersal eggs is apparently of such short duration that even newly hatched larvae were rarely collected below 100 m. However, this does not appear to be the case for walleye pollock, which spawn at depths greater than 200 m in Shelikof Strait, with mean depths of eggs and yolk-sac larvae generally greater than 100 m (Kendall and Kim, 1989; Kendall et al.[1]).

The diel vertical distribution pattern that we observed for several taxa is not the pattern typically observed for most ichthyoplankton and for zooplankton in general. The more common pattern, termed a 'Type I' migration (Neilson and Perry, 1990), involves a nocturnal ascent into surface waters and is undertaken by larvae of a diversity of fish species.

Table 3

Weighted mean depths (m) and standard deviations of the mean depths (in parentheses) for each taxon and for all larvae excluding walleye pollock by time of day and overall depth for all times combined. Also given are the results of the ANOVAs testing for diel differences in weighted mean depth and the significant ($P< 0.05$) Tukey multiple-comparison tests between time periods.

Dawn	Day	Dusk	Night	Overall	*F*-value	Tukey test
All Larvae (excluding walleye pollock)						
16.59 (2.72)	17.46 (1.52)	15.45 (2.25)	25.74 (1.52)	21.75 (1.87)	33.17***	Night>Day=Dawn=Dusk
Hippoglossoides elassodon						
14.82 (0.63)	16.94 (2.73)	10.80 (0.42)	20.10 (0.05)	18.06 (1.33)	31.89***	Night>Day=Dawn>Dusk
Ammodytes hexapterus						
31.21(11.45)	27.67 (4.59)	22.67 (2.38)	37.51 (4.45)	32.85 (3.39)	6.05**	Night>Dusk=Day
***Bathymaster* spp.**						
8.21 (0.11)	11.25 (0.08)	11.28 (1.08)	37.95 (2.84)	18.12 (6.05)	441.48***	Night>Dusk, Day>Dawn
Pleuronectes bilineatus						
—	19.75 (1.83)	—	30.73 (1.63)	25.47 (4.64)	128.36***	Night>Day
Gadus macrocephalus						
—	20.36(10.35)	—	24.92 (0.12)	22.12 (6.56)	1.14 n.s.	

*** $P<0.001$
** $P<0.01$
n.s. $P>0.05$.

However, the reverse pattern ('Type II' migration), although less frequently documented, has been observed for larvae of several fish species, including many of the taxa we examined. For example, Boehlert et al. (1985) observed larval *G. macrocephalus* at lower depths at night than during the day off the Oregon coast. Walline[5] found that *Bathymaster* spp. in the Bering Sea generally migrated downward at night. Larvae of *A. hexapterus* collected in bays around Kodiak Island were concentrated from 10 to 30 m during the day but were found at lower depths at night (Rogers et al.[6]), and larvae of a congener (*A. personatus*) collected off Japan also exhibited reverse migration (Yamashita et al., 1985). Rogers et al.[6] and Pritchett and Haldorson (1989) found that rock sole (*P. bilineatus*), as well as larvae of several other taxa, showed reverse diel migrations during the spring.

We believe that sampling bias could not have resulted in the observed reverse distributions. Eggs of *H. elassodon*, as expected, showed no differences by time of day in our study and walleye pollock larvae in these same collections exhibited a normal diel migration pattern (Type I), occurring mainly in the 30–45 m range during daytime and above 30 m at night (Kendall et al.[1]; see also Kendall et al., 1987). Net avoidance, although suggested by the higher night catches overall as well as the larger mean size of larvae collected at night, is not a plausible explanation for the observed diel pattern. Light-aided daytime avoidance would be expected to influence the catch of larvae in the surface strata more than those in deeper strata, thus leading to underestimates of near-surface daytime abundances and the magnitude of reverse migration.

The prevalence of the reverse diel migration pattern in our study suggests an adaptive role for this behavior. Temperature gradients are relatively minor (<1°C) over the upper 50–60 m where most of the migration occurs (Fig. 7), and the majority of the larvae appear to be above the seasonal thermocline at all times of the day. Thus, we see no possibility of temperature-mediated energetic advantage related to migration at any time of the day. Similarly, observed density gradients are not pronounced (<0.5 σ_t units) within this surface layer (Fig. 7; Kendall et al.[1]) and there appears to be no physical mechanism that would aggregate either

Table 4

Results of two-way ANOVAs testing for differences in density of larvae by depth and time of day.

Source of variation	df	Sum of squares	Mean square	*F*-ratio	*P*-value
All larvae (excluding walleye pollock)					
Time	3	14.60	4.86	9.85	0.00
Depth	6	51.63	8.61	17.40	0.00
Time × depth	18	14.11	0.78	1.58	0.05
Error	4868	2406.73	0.49		
Hippoglossoides elassodon					
Time	3	4.97	1.66	0.48	0.69
Depth	6	93.59	15.60	4.54	0.00
Time × depth	18	15.49	0.86	0.25	0.99
Error	116	398.59	3.44		
Ammodytes hexapterus					
Time	3	55.08	18.36	11.70	0.00
Depth	6	94.13	15.69	9.99	0.00
Time × depth	18	34.27	1.90	1.21	0.26
Error	116	182.03	1.57		
***Bathymaster* spp.**					
Time	3	8.84	2.95	1.24	0.30
Depth	6	44.33	7.39	3.10	0.01
Time × depth	18	21.35	1.19	0.49	0.96
Error	116	276.73	2.39		
Pleuronectes bilineatus					
Time	1	1.68	1.68	1.35	0.25
Depth	6	19.01	3.17	2.55	0.03
Time × depth	6	3.47	0.58	0.47	0.83
Error	69	85.78	1.24		
Gadus macrocephalus					
Time	1	9.12	9.12	4.09	0.05
Depth	6	22.46	3.74	1.68	0.14
Time × depth	6	7.06	1.18	0.53	0.79
Error	69	153.81	2.23		

[5] Walline, P. D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June–July 1979. NWAFC Processed Rep. 81-05, 22 p.

[6] Rogers, D. E., D. J. Rabin, B. J. Rogers, K. J. Garrison, and M. E. Wangerin. 1979. Seasonal composition and food web relationships of marine organisms in the nearshore zone of Kodiak Island including ichthyoplankton, meroplankton (shellfish), zooplankton and fish. Univ. Washington, Fish. Res. Inst. Rep. FRI-UW-7925, 291 p.

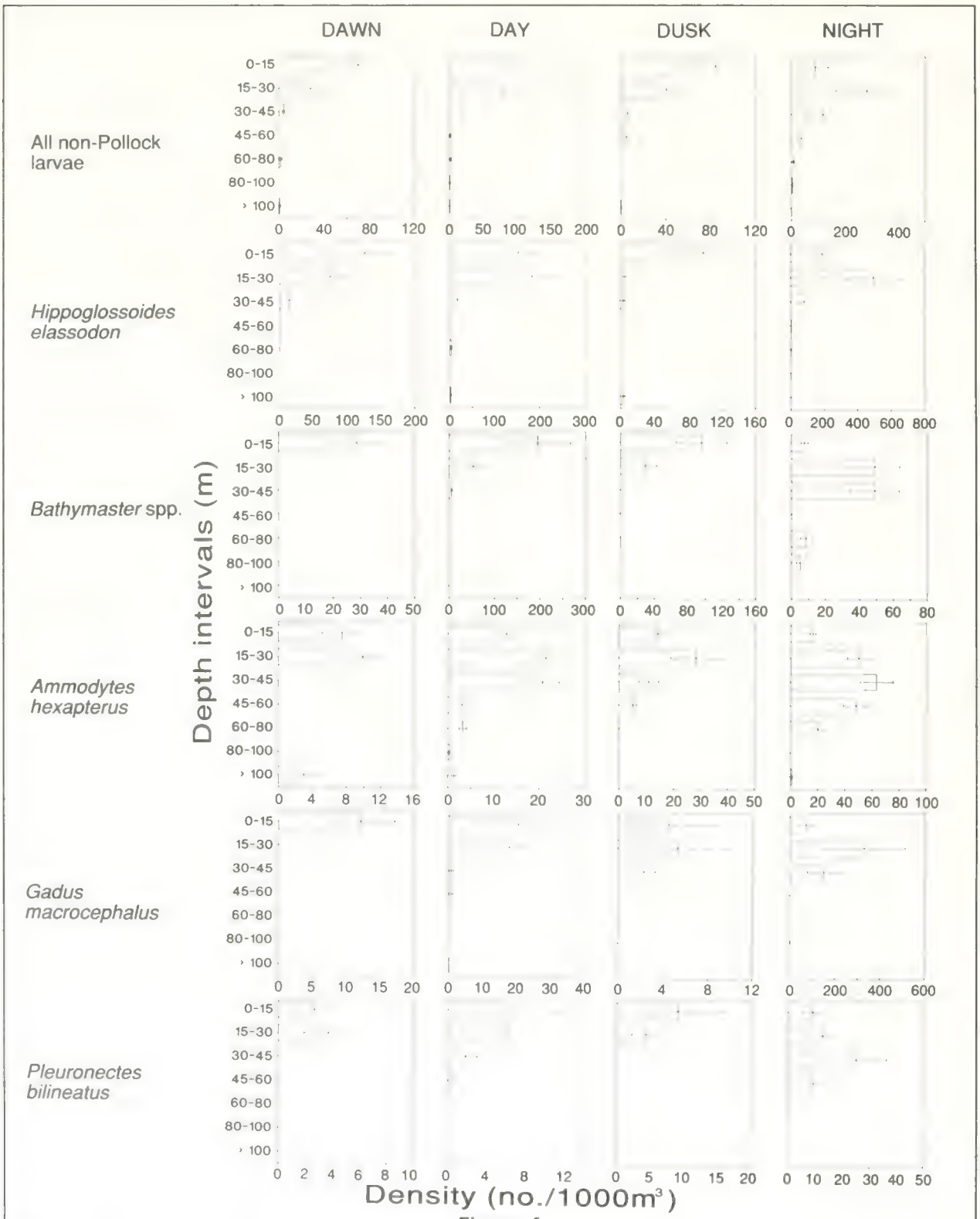

Figure 4

Diel changes in the vertical distribution of all larvae (excluding walleye pollock), and *Hippoglossoides elassodon*, *Bathymaster* spp., *Ammodytes hexapterus*, *Gadus macrocephalus*, and *Pleuronectes bilineatus* larvae. Bars are mean abundances per 1000 m^3 at each depth interval and error bars are ± one standard deviation about the mean abundance.

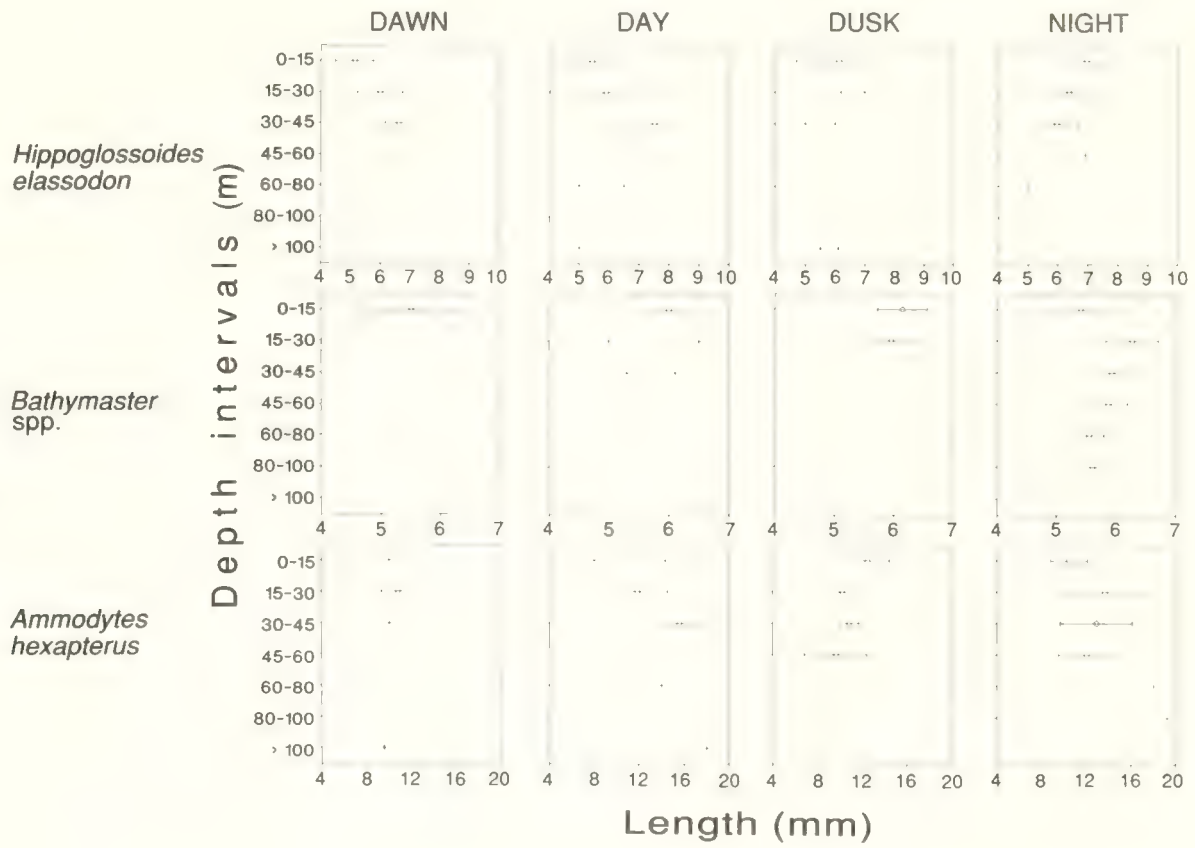

Figure 5

Diel vertical distribution of larval lengths of *Hippoglossoides elassodon*, *Bathymaster* spp., and *Ammodytes hexapterus*. Circles are mean length at each depth interval and error bars are ± one standard deviation about the mean length. The plus signs indicate actual lengths measured when less than three lengths were available from a particular depth stratum.

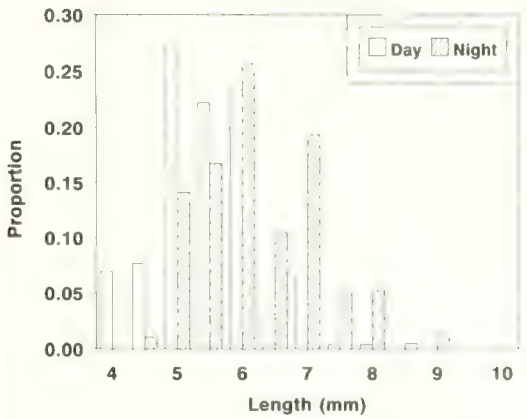

Figure 6

Day versus night proportional length distributions of *Hippoglossoides elassodon* larvae.

larvae or their prey at certain depths or inhibit them from migrating to different depths.

The fact that walleye pollock larvae, which are the dominant fish larvae in this area representing 70–80% of the larvae present in Shelikof Strait in the spring (Rugen[7]; this study), show a normal migration pattern (Kendall et al., 1987) suggests one potential explanation for reverse migration patterns of other larvae. If other larvae feed on the same microzooplankton prey as larval walleye pollock and these prey resources were limiting, then the presence of these other larvae in surface waters at different times of the day than those of walleye pollock would reduce competition with the numerically dominant taxon. Copepod nauplii, an important

[7] Rugen, W. C. 1990. Spatial and temporal distribution of larval fish in the Western Gulf of Alaska, with emphasis on the period of peak abundance of walleye pollock (*Theragra chalcogramma*) larvae. NWAFC Processed Rep. 90-01, 162 p.

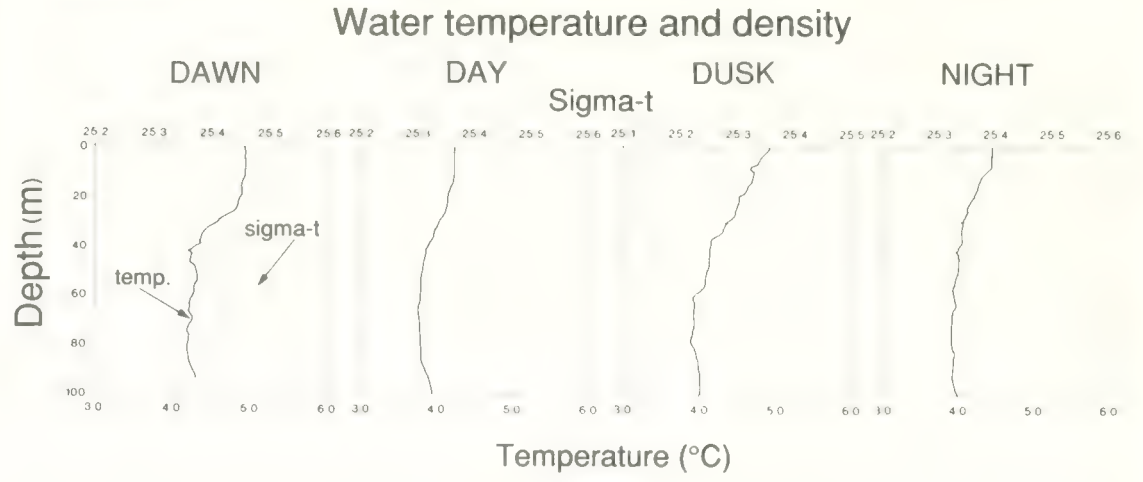

Figure 7

Diel vertical profiles of temperature and density (σ_t). Data are means of at least four casts within each time interval and were collected at 1 m depth intervals.

component of the diet of many larval fishes including walleye pollock (Kendall et al., 1987), were the most abundant microzooplankton category found in Shelikof Strait, mostly in the upper 30 m during May 1986 and 1987 (Incze and Ainaire[8]). During diel Series 4, copepod nauplii had overall mean depths between 20 and 34 m but showed no obvious diel pattern in depth distribution (Kendall et al.[1]). Although feeding at a different time of day from walleye pollock might reduce interference competition (i.e. behavioral interactions) with the dominant species, it is highly unlikely, based on typical larval fish and copepod naupliar densities, that prey resources could ever be depleted by larval fish (Cushing, 1983; MacKenzie et al., 1990). Moreover, if food were limiting, then it would be advantageous for all larvae to stay in the layer of maximum food concentration throughout the diel period to maximize total intake. Thus, we do not see a trophic benefit accruing from a reverse migration pattern for these larvae.

If feeding by these larvae is periodic and dependent on some minimum light level, then the vertical distribution pattern can be partially explained by larval feeding response. Assuming light levels were limiting feeding at depths below 30 m, then it would be necessary for larvae to ascend to a shallower depth during the daytime when light is at a maximum. Following the cessation of feeding at dusk, larvae would be expected to become inactive and passively sink to deeper levels at night. Such a mechanism has been postulated for Japanese sand lance (*A. personatus*) by Yamashita et al. (1985) who demonstrated a nocturnal cessation of feeding in this species. Although we lack data on the diel feeding chronology of any of the taxa examined here, it is possible that feeding occurs mainly in the crepuscular periods, with a temporary cessation of ingestion occuring during midday as observed in the field for larval walleye pollock (Canino and Bailey[9]). The shallowest mean depth occurs at either dawn or dusk for the three common species that were examined over the four time periods with slightly greater depths occurring during midday. If larvae were not feeding during the middle of the day, it would be advantageous to cease swimming altogether and sink through the water column to avoid being sensed by mechanoreceptive or visual predators. Following a particular isolume would produce a similar daytime pattern but could not account for the deeper distribution at night that we observed. Larval walleye pollock in the laboratory have been shown to avoid high light levels (Olla and Davis, 1990) but they also require relatively low light levels to initiate feeding (Paul, 1983). Unfortunately, we have no data available on the light levels necessary for feeding in the taxa we examined with which we can evaluate this hypothesis.

[8] Incze, L. S., and T. Ainaire. In review. Zooplankton of Shelikof Strait, Alaska. I. Micro-zooplankton prey of larval pollock, *Theragra chalcogramma*. Submitted to Fish. Bull.

[9] Canino, M. F., and K. M. Bailey. In review. Gastric evacuation of walleye pollock, *Theragra chalcogramma* (Pallas), larvae in response to feeding. Submitted to Journal of Fish Biology.

A potential disadvantage to a diurnal ascent is increased susceptibility to visually feeding planktivorous fishes. However, acoustic and trawl survey data suggest that epipelagic fish predators are rare during the spring in this area and the majority of the nekton biomass is found in midwater or near the bottom (Brodeur et al., 1991), well below the depth of most larvae. On the other hand, euphausiids, which are possibly the major invertebrate predator on walleye pollock yolk-sac larvae, undergo a nocturnal ascent to surface water and descend to greater depths during the day in Shelikof Strait (Bailey et al., 1993). If euphausiids were also predators on non-pollock larvae and feed only in the surface layer above the nighttime depths of these larvae, then a distinct advantage would be conferred upon individuals adopting a reverse diel migration pattern, as has been postulated for copepods (Ohman et al., 1983; Ohman, 1990). Based on field and experimental results, it has become increasingly apparent that predators can alter the diel vertical distribution patterns of invertebrate prey (Ohman et al., 1983; Gliwicz, 1986; Bollens and Frost, 1989; Levy, 1990; Neill, 1990; Frost and Bollens, 1992), but evidence for this effect on larval fish as prey is presently lacking.

Although a variation in depth by time of day was apparent for all species and consistent among species, it was not substantial enough to be statistically significant in all cases (e.g. *G . macrocephalus*). This may be due in part to the lack of resolution of our sampling intervals. The smallest average migration that we could detect is ~15 m; thus, diel vertical migrations less than that were not likely to be detected. Although a daily ambit of 30 m is not exceptional for larger larvae, it may be excessive for newly hatched individuals. For a study specifically examining the diel vertical distribution of the species considered here, we recommend sampling with a multiple net system every 5 m over the upper 40 m of the water column. Some bias may have also resulted from combining tows from different years, weeks, or geographic areas into our four time periods, which was necessitated by the relatively low occurrence rate and densities of these taxa. However, the remarkably strong and consistent diel differences among the different taxa, despite this introduced sampling variability, lend credence to our findings.

If there was differential migration by size classes of larvae, this condition might also obscure some of our results. The vertical distribution of larval lengths of the dominant species did not show any consistent patterns by time of day. The mean length by depth varied significantly for *H. elassodon*; smaller larvae were found at greater depths during the daytime and at the surface at night. This cannot be explained by visual gear avoidance alone since the nighttime pattern would then be expected to be random rather than exhibit the increasing mean length with depth that we observed. A possible explanation for this pattern might be that larger larvae may migrate a greater distance than smaller larvae, a pattern frequently observed in other fish larvae (Neilson and Perry, 1990). It is also possible that the migration of different size classes is asynchronous (Pearre, 1979). However, the available size ranges of the dominant species in our data was not extensive enough to examine diel migration patterns of different size classes. Moreover, caution should be exercised in examining larval length data in multiple net systems. Since larvae shrink upon death (Theilacker, 1980; Hay, 1981) and the likelihood of death may be related to time in net, we may assume that larvae caught in the first (deepest) net may have undergone more shrinkage than those in the last (surface) net.

In conclusion, this study shows that all the common larvae exhibit a reverse vertical migration pattern, opposite to that of the overall dominant species, walleye pollock. In Auke Bay, an inland embayment in Southeast Alaska (58°22' N) on the eastern side of the Gulf of Alaska, Haldorson et al. (1993) found a Type I migration for the numerically dominant osmerid larvae in their sampling and a Type II migration for the five next most abundant taxa (*T. chalcogramma*, *H. elassodon*, *P. bilineatus*, *Leuroglossus schmidti*, and Agonidae). These authors attribute this diel-depth distribution pattern to temperature preferences by each species, although their vertical temperature gradients were more pronounced than what we observed in our study. Since most abiotic variables (other than light intensity) and food resources varied little over the depths through which much of the migration occurred in Shelikof Strait, we hypothesize that the reverse migration pattern that we documented was either a predator-avoidance mechanism or else an optimization of light levels for feeding. The prevalence of reverse migration in this and other studies suggests that it may be more common than previously suspected, especially in higher latitude ecosystems, and the factors contributing to this phenomenon merit further investigation.

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Literature cited

Ahlstrom, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish. Wild. Serv., Fish. Bull. 60:107–146.

Bailey, K. M., R. D. Brodeur, N. Merati, and M. M. Yoklavich.
1993. Predation on walleye pollock (*Theragra chalcogramma*) eggs and yolk-sac larvae by pelagic crustacean invertebrates in the western Gulf of Alaska. Fish. Oceanog. 2:30–39.

Boehlert, G. W., D. M. Gadomski, and B. C. Mundy.
1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull. 83:611–621.

Bollens, S. M., and B. W. Frost.
1989. Predator-induced diel vertical migration in a planktonic copepod. J. Plankton Res. 11:1047–1065.

Brewer, G. D., and G. S. Kleppel.
1986. Diel vertical distribution of fish larvae and their prey in nearshore waters of southern California. Mar. Ecol. Prog. Ser. 27:217–226.

Brodeur, R. D., K. M. Bailey, and S. Kim.
1991. Cannibalism on eggs by walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Mar. Ecol. Prog. Ser. 71:207–218.

Cushing, D. H.
1983. Are fish larvae too dilute to affect the density of their food organisms? J. Plankton Res. 847–854.

de Lafontaine, Y., and D. Gascon.
1989. Ontogenetic variation in the vertical distribution of eggs and larvae of Atlantic mackerel (*Scomber scombrus*). Rapp. P.-v. Réun. Cons. int. Explor. Mer 191:137–145.

Frost, B. W., and S. M. Bollens.
1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. Can. J. Fish. Aquat. Sci. 49:1137–1141.

Gliwicz, M. Z.
1986. Predation and the evolution of vertical migration in zooplankton. Nature 320:746–748.

Haldorson, L., M. Prichett, A. J. Paul, and D. Ziemann.
1993. Vertical distribution and migration of fish larvae in a Northeast Pacific bay. Mar. Ecol. Prog. Ser. 101:67–80.

Hay, D. E.
1981. Effects of capture and fixation on gut contents and body size of Pacific herring larvae. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:395–400.

Incze, L. S., P. B. Ortner, and J. D. Schumacher.
1990. Microzooplankton, vertical mixing and advection in a larval fish patch. J. Plankton Res. 12:365–379.

Kamba, M.
1977. Feeding habits and vertical distribution of walleye pollock, *Theragra chalcogramma* (Pallas), in early life stage in Uchiura Bay, Hokkaido. Res. Inst. N. Pac. Fish., Hokkaido Univ., Spec. Vol., p. 175–197.

Kendall, A. W., Jr., and S. Kim.
1989. Buoyancy of walleye pollock (*Theragra chalcogramma*) eggs in relation to water properties and movement in Shelikof Strait, Gulf of Alaska. *In* R. J. Beamish and G. A. McFarlane (eds.), Effects of ocean variability on recruitment and evaluation of parameters used in stock assessment models, p. 169–180. Can. Spec. Pub. Fish. Aquat. Sci. 108.

Kendall, A. W., Jr., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert.
1987. Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska. Fish. Bull. 85:499–521.

Kerfoot, W. C.
1985. Adaptive value of vertical migration: comments on the predation hypothesis and some alternatives. Contrib. Mar. Sci. 27:91–113.

Lampert, W. H.
1989. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. 3:21–27.

Laprise, R., and J. J. Dodson.
1993. Nature of environmental variability experienced by benthic and pelagic animals in the St. Lawrence Estuary, Canada. Mar. Ecol. Prog. Ser. 94:129–139.

Lenarz, W. H., R. J. Larson, and S. Ralston.
1991. Depth distributions of late larvae and pelagic juveniles of some fishes of the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 32:41–46.

Levy, D. A.
1990. Reciprocal diel vertical migration behavior in planktivores and zooplankton in British Columbia lakes. Can. J. Fish. Aquat. Sci. 47:1755–1764.

MacKenzie, B. R., W. C. Leggett, and R. H. Peters.
1990. Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the field? Mar. Ecol. Prog. Ser. 67:209–225.

Matarese, A. C., A. W. Kendall Jr., D. M. Blood, and B. M. Vinter.
1989. Laboratory guide to early life history stages of Northeast Pacific fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 80, 652 p.

Neill, W. E.
1990. Induced vertical migration in copepods as a defence against invertebrate predation. Nature 345:524–526.

Neilson, J. D., and R. I. Perry.
1990. Diel vertical migrations of marine fishes: an obligate or facultative process? Adv. Mar. Biol. 26:115–168.

Ohman, M. D.
1990. The demographic benefits of diel vertical migration by zooplankton. Ecol. Monogr. 60:257–281.

Ohman, M. D., B. W. Frost, and E. B. Cohen.
1983. Reverse diel vertical migration: an escape from invertebrate predators. Science 220:1404–1407.

Olla, B. L., and M. W. Davis.
1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser. 63:105–112.

Paul, A. J.
1983. Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 13:175–179.

Pearre, S.
1979. Problems in the detection and interpretation of vertical migration. J. Plankton Res. 1:29–44.

Pritchett, M., and L. Haldorson.
1989. Depth distribution and vertical migration of larval walleye pollock (*Theragra chalcogramma*). *In* Proceedings of the international symposium on the biology and management of walleye pollock, November 14–16, 1988, Anchorage, Alaska, p. 173–183. Alaska Sea Grant Rep. 89-1, Univ. Alaska, Fairbanks.

Theilacker, G. H.
1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull. 78:685–692.

Wiebe, P. D., K. H. Burt, S. H. Boyd, and A. W. Morton.
1976. A multiple opening/closing net and environmental sensing system for zooplankton. J. Mar. Res. 34:313–326.

Yamashita, Y., D. Kitagawa, and T. Aoyama.
1985. Diel vertical migration and feeding rhythm of the larvae of the Japanese sand-eel *Ammodytes personatus*. Bull. Japan. Soc. Sci. Fish. 51:1–5.

Changes in a population of orange roughy, *Hoplostethus atlanticus*, with commercial exploitation on the Challenger Plateau, New Zealand

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Abstract.—The commercial fishery for orange roughy on the Challenger Plateau developed in 1981, increased markedly throughout the mid-1980s, and then declined rapidly by 1990. Data from research trawl surveys and commercial fishing returns over the period are examined, and changes in the population are described.

The distribution of orange roughy changed over the period examined; there was a contraction of the areas of high density and apparent fishing-out of aggregations on relatively flat bottom. Aggregations are now largely confined to pinnacles. Biomass of orange roughy, measured by bottom trawl survey indices and commercial catch per unit of effort, declined substantially and is currently estimated to be about 20% of virgin levels. Most other incidental species in the trawl surveys have also declined in abundance, and there are no indications of 'species replacement.'

Data on size, reproductive stage, size at maturity, and feeding have also been examined. Size structure of the population has not changed over time. Time of spawning (July) and the pattern of gonad development have been consistent over the years. Diet composition has also remained similar; dominant prey groups are natant decapod crustaceans and small fish.

It is suggested that biological changes have not been apparent because orange roughy are a long-lived, slow-growing species, with low productivity. There could be a long response time to fishing pressure, yet orange roughy populations can be quickly reduced to low levels by commercial fishing.

Orange roughy (*Hoplostethus atlanticus* Collett) has a worldwide distribution on the continental slope at depths of 700 to 1,500 m. However, it is fished commercially only off New Zealand, Australia, and in the northeastern Atlantic Ocean. The New Zealand fishery is the most established, having started in 1978; the others date from 1988 and 1991, respectively. Orange roughy is one of the most valuable commercial species in New Zealand waters, with annual landings of 40–50,000 metric tons (t) and export earnings of NZ $100–150 million (Robertson, 1991).

The New Zealand fishery for orange roughy occurs in a number of areas (Fig. 1), including the Challenger Plateau, a broad submarine plateau off the west coast of New Zealand. The commercial fishery on the Plateau developed in late 1981 and rapidly expanded into one of the most important orange roughy fisheries in New Zealand waters, with annual catches up to approximately 16,000 t (Table 1). The fishery operates primarily during winter (June–August), when the fish form large spawning aggregations at depths of 850–900 m (Clark, 1991a).

The fishery has been managed by a Total Allowable Catch (TAC) system since 1982. Tracey et al. (1990) and Clark (1991a) discussed details of this management regime. Initially, catches were limited to 7,000 t by the TAC for all areas of the New Zealand Exclusive Economic Zone (EEZ), outside the established fishing grounds on the east coast. A TAC of 4,950 t was set for 1983–84 and 1984–85 (October–September fishing year) on the Challenger Plateau and west coast of the South Island. This was raised to 6,190 t specifically for the Challenger fishery in 1985–86 based on biomass estimates from a trawl survey in winter 1984. The quota was raised to 10,000 t in 1986–87, and further to 12,000 t in 1987–88, in order to assess the effects of heavier fishing on the population dynamics of orange roughy ("adaptive management"). In the following fishing year only 8,200 t of quota were allocated, the rest withheld because of signs that the orange roughy population was declining rapidly. During 1989–90 the TAC was reduced to 2,500 t after new stock assessments showed the population was overexploited and had declined to low levels (Clark and Francis, 1990). The TAC was further reduced for 1990–91 to promote rebuilding of the population.

These changes occurred against a background of increasing infor-

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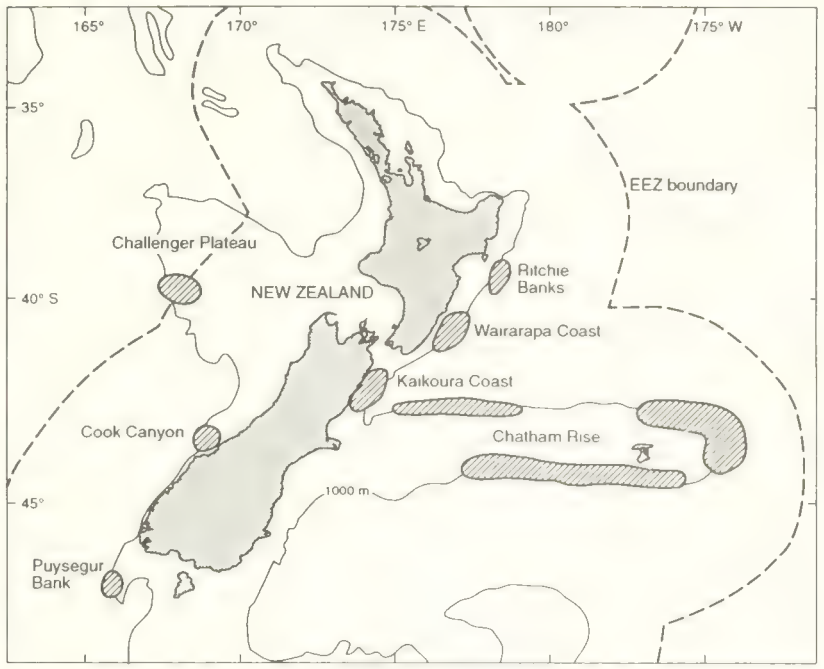

Figure 1

Map of New Zealand and offshore waters of the Exclusive Economic Zone (EEZ), showing the location of the Challenger Plateau and other major fishing areas for orange roughy (*Hoplostethus atlanticus*).

Table 1

Reported catches (t) of orange roughy (*Hoplostethus atlanticus*) from the Challenger Plateau (ORH 7A and outside EEZ) (from Clark 1992; total estimated catch includes allowance for research survey catches and a correction for 15–30% under-estimation of true catch in reported catch figures because of burst trawls, fish discards, and incorrect official conversion factor).

Fishing year (Oct–Sept)	Total reported catch	Total estimated catch	TAC
1980/81	33	43	
1981/82	4,248	5,522	
1982/83	11,839	15,409	
1983/84	9,527	12,514	4,950
1984/85	5,117	6,707	4,950
1985/86	7,753	10,251	6,190
1986/87	11,492	15,750	10,000
1987/88	12,181	15,830	12,000
1988/89	10,241	12,627	12,000[1]
1989/90	4,309	5,171	2,500
1990/91	1,357	1,560	1,900

[1] 8,219 t allocated.

mation on orange roughy. It has only recently been realized that orange roughy is very slow-growing and long-lived. Mace et al. (1990) recorded a growth rate of about three cm per year for the first four years of life (validated ages), and an estimated age at maturity of 24 years and maximum age over 50 years. They estimated natural mortality to be low (less than 0·1 yr^{-1}) and concluded that sustainable yields of orange roughy would be relatively low and show slow recovery from over-fishing. Recent estimates of the maximum age of orange roughy from Australian waters approach 150 years (Fenton et al., 1991).

Quotas for orange roughy harvest from New Zealand have been reduced in recent years on the basis of information which suggests much lower productivity than originally assumed. However, the Challenger Plateau population had already declined markedly and provides some insight into the effects of heavy fishing pressure on orange roughy population dynamics.

There is an extensive literature on general responses of fish populations to exploitation, covering lake ecosystems (e.g. Regier and Loftus, 1972; Spangler et al., 1977), coral reef fisheries (e.g. Russ and Alcala, 1989), and relatively shallow-water marine environments (e.g. Hempel, 1978; Pauly, 1979; Grosslein et al. 1980). There have been few studies on deep-water or long-lived species such as orange roughy. The closest is probably Pacific ocean perch (*Sebastes alutus*) which is found at depths to 600 m in the North Pacific Ocean and has a maximum age of 90 years (e.g. Gunderson, 1977; Leaman, 1991).

There are a number of general population responses to exploitation, which include

1 Decline in abundance of fished species.
2 Contraction of distribution or areas of high density.
3 Change in age structure or size structure, or both, with fewer old, large fish and the population dominated by new recruits.
4 Increase in growth rate of individuals, with a decrease in age for a given length.
5 Lower age at maturity or size at maturity, or both.

6 Possible change in species composition over time ('species replacement').

Such responses are often observed in short-lived, fast-growing species (e.g. Pauly, 1979; Grosslein et al., 1980). Some have also been noted with *Sebastes alutus* (Gunderson, 1977; Leaman, 1991), but it is not clear whether these changes would occur in such a long-lived species as orange roughy, or over what time period such changes would become apparent. Orange roughy on the Challenger Plateau have been exploited for only 10 years, and hence it seems unlikely that marked changes in biological characteristics could occur over such a relatively short time period in relation to the longevity of the species. Therefore, we might expect to observe changes in biomass and distribution, as well as age and size structure of the population, but not changes in growth rate or reproductive potential.

In this paper, we summarize some of the available data on distribution, abundance, and biology of orange roughy on the Challenger Plateau, primarily over the period 1984–90. This period covers the early years of the developing fishery, to maximum levels of exploitation, and subsequent decline of the population. We describe the reduction in size and distribution of the stock and investigate associated changes in size structure, aspects of reproduction, and feeding.

Methods

Research trawl surveys

Trawl surveys have been carried out in the winter (June–July) of each year from 1984 to 1990. The vessel used, area covered, intensity of trawling, and survey design differed between years, and all are not directly comparable (Table 2). Surveys from 1987 to 1989 were treated as fully comparable, but only selected data have been used from other surveys: distribution from 1984 and 1990, and biology (size, reproductive, and feeding data) from 1984, 1985, 1986, and 1990.

The general survey design was two–phase stratified random (after Francis, 1984). The survey area was divided into a number of strata based on depth and certain bottom features (e.g. pinnacles). General stratification is shown in Figure 2. The depth range covered was 800 to 1,200 m. New, random station positions within strata were selected each year, except in strata 10 and 11 on pinnacles where a random tow direction was adjusted to avoid untrawlable ground, and these trawls were repeated each year. A similar net design and gear set up was used for each survey. Tow length was standardized where possible at 1.5 nautical miles (nmi). Trawling speed was 3.0–3.5 knots.

Biomass indices were calculated by the area swept method as described by Francis (1981). Biomass and its standard error were calculated from the following formulae:

$$B = \sum (X_i a_i)/cb$$

and

$$S_B = \sqrt{\sum s_i^2 a_i^2 / c^2 b^2} \ ,$$

where B is biomass (t), X_i is the mean catch rate (kg·km^{-1}) in stratum i, a_i is the area of stratum i (km^2), b is the width swept by the gear (defined as doorspread (m) by MAF Fisheries), c is the catchability coefficient (an estimate of the proportion of fish available to be caught by the net), S_B is the standard error of the biomass, s_i is the standard error of X_i

The catchability coefficient was assigned a value of 0.27, which represents the wingend spread divided by the doorspread, because orange roughy form schools which are not believed to be herded substantially by doors or sweeps.[1]

Approximate 95% confidence limits (CL) were calculated as

$$\mathrm{CL} = B \pm 2S_B .$$

[1] Orange Roughy Working Group, MAF Fisheries, Greta Point, P.O. Box 297, Wellington, New Zealand, pers. commun. 1991.

Table 2

Trawl surveys carried out on the Challenger Plateau for orange roughy (*Hoplostethus atlanticus*).

Vessel	Year	Date	Area (km^2)	Number of trawls	Survey design
Arrow	1984	3/7–18/7	11,956	118	2 phase SRTS[1]
Arrow	1985	4/7–20/7	209	16	1 phase SRTS
Arrow	1986	4/7–17/7	94	10	transect grid
Amaltal Explorer	1987	18/6–13/7	8,270	129	2 phase SRTS
Amaltal Explorer	1988	4/7–24/7	8,270	85	2 phase SRTS
Amaltal Explorer	1989	8/7–30/7	8,270	160	2 phase SRTS
Will Watch	1990	7/7–29/7	8,270	141	2 phase SRTS

[1] Stratified random trawl survey

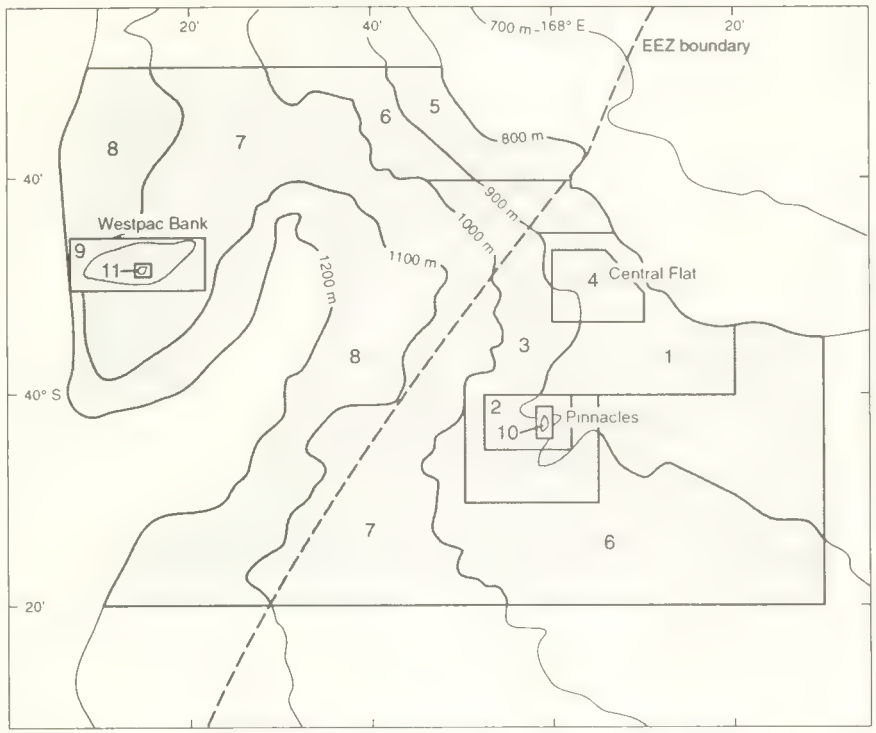

Figure 2

The Challenger Plateau survey area, showing bathymetry (depth contour in m) and details of survey stratification.

The coefficient of variation (CV) is a measure of the precision of the biomass estimate, and was calculated by

$$CV = S_B / B \times 100.$$

Stock reduction analysis

A stock reduction technique was used to estimate virgin biomass based on the method of Francis (1990, 1992). This incorporated a complete catch history for the stock, a time series of abundance indices, and life history parameters used in a deterministic age–structured population model (see Clark, 1992). The latter were the von Bertalanffy growth parameters (L_∞=39.5 cm, k=0.059·yr^{-1}, t_0 = –0.3 yr), natural mortality=0.04·yr^{-1}, weight-length parameters (a=0.0963, b=2.68), age at maturity (24 yr), age at entry to the fishery (24 yr), and Beverton-Holt recruitment steepness of 0.75.

Five sets of abundance indices were used from trawl surveys between 1984 and 1990, and commercial catch per unit of effort (CPUE) data (unstandardized mean catch per tow by monthly groupings):

1 CPUE in winter months (June–September) from 1983 to 1989. This covered the period of development of the fishery through to maximum exploitation. It is felt that the fishery was not constrained much by the TAC over this time.
2 CPUE in winter months from 1983 to 1991. This includes data from 1990 and 1991, following a substantial reduction in TAC and effort.
3 CPUE in non-winter months from 1983 to 1991.
4 Trawl survey indices from 1987 to 1989. These surveys covered the same area, had the same design, and used the same vessel.
5 Trawl survey indices from 1984 and 1987 to 1990. This series incorporated data from a smaller area surveyed in 1984 and from the 1990 survey, both of which used a different vessel from 1987 to 89.

The maximum likelihood method was used to estimate virgin biomass. Ninety-five percent confidence intervals were estimated by using bootstrapping techniques with the coefficient of variation fixed at 20%. The best estimate of virgin biomass was then used in an age-structured model (detailed in Francis, 1992) to estimate current biomass.

Biological data

Standard procedure during trawl surveys was to take a random sample of about 200 fish from each tow. These were measured (standard length rounded down to the nearest whole cm [standard MAF Fisheries procedure]) and sexed. Twenty of these fish were randomly selected, their otoliths extracted, and more detailed data collected: standard length (rounded down to the nearest whole mm), weight (rounded down to the nearest gm), sex, stage of gonad maturity (see below), gonad weight (rounded down to the nearest gm), fullness of stomach, state of digestion of contents, and stomach contents (to species level where possible).

Size Length-frequency distributions have been constructed to represent the total population where possible. In the years 1984 and 1987–90, data have

been scaled by percentage sampled to represent each catch and further scaled by stratum biomass to approximate the population. Samples in 1985 and 1986 were scaled to represent solely the catch, as survey design was inadequate for biomass estimation.

Length-frequency data are difficult to compare statistically and, for the purposes of this study, have not been attempted. However, to enable a general comparison, a single distribution was constructed combining length-frequency data from all years weighted by the number of tows each year. This distribution is plotted together with those from each year separately.

Mean size by sex was calculated separately for three main regions of spawning within the survey area (strata 1, 4; 10; 9, 11) as it was unlikely these areas had been fished equally (see later 'Commercial Fishery' section). The sample sizes used in calculating the standard error were number of tows, not number of fish. Orange roughy can associate in size groups; between-tow variance was greater than within-tow variance. Variance is represented by ±2.0 standard errors for all years except 1986, when ±2.2 standard errors was arbitrarily used because there were only 10 trawls.

Reproduction Macroscopic staging of reproductive condition followed Pankhurst et al. (1987):

Stage	Female	Male
1	Immature/resting	Immature/resting
2	Early maturation	Early maturation
3	Maturation	Maturation
4	Ripe	Ripe/running ripe
5	Running ripe	Spent
6	Spent	–

Relative frequency of gonad stages was examined. Analyses were based on the samples taken. They were not scaled in any way, as there were no apparent differences between the length frequencies of the samples and the distribution of the total population. Only data from females are presented, as their macroscopic gonad stages can be determined more accurately than those from males.

Size at maturity was determined from samples taken over the total survey area using a 'probit analysis' approach (after Pearson and Hartley, 1976). It was assumed that length at maturity is normally distributed in the population. The regression part of the analysis was repeated 10 times to ensure convergence of the estimate.[2] A standard linear regression analysis was carried out on results to investigate trends over time by using the SAS statistical package (SAS, 1988).

Feeding Data on frequency of occurrence were available from all surveys. Frequency of occurrence was defined as the number of stomachs in which a food item occurs, expressed as a proportion of the total number of stomachs containing food. Only stomachs with part-full or full classifications, and with fresh or partly digested contents, were included in analyses.

Commercial fishing data

Data on the catch and position of each tow and the start and finish times have been collected since 1980. However, catch and effort information is difficult to standardize and interpret for orange roughy. Fish can be highly aggregated at various times of the year, and 'windows' or escape panels in the net are frequently used to reduce catch size and minimise damage to nets. Fishing performance varies with experience of skipper and crew, and technology has advanced considerably in recent years (in particular, development of Global Positioning System navigation, which enabled improved accuracy when fishing pinnacles). Fishing logbooks often do not have accurate information on length of tow on the bottom. Fishing for orange roughy on the Challenger Plateau occurs on a variety of bottom terrain: on flat bottom, in troughs and steep slope, and on the tops and sides of pinnacles. In each case, the effective fishing time and fishing technique differ greatly, and they are almost separate types of fisheries. In order to gain an indication of trends in catch rates, data were examined on the basis of mean catch per tow for two size classes of vessel (20–60 m, generally domestic fresh fish boats; and 60–90 m, domestic factory trawlers). Catch per unit of effort (CPUE) values were similar for both classes, and so data here are combined. Monthly data were amalgamated into two time periods: first, 'winter' (June, July, August) which covers the spawning period; second, 'out of season' (all other months). This division represents two distinct phases of orange roughy distribution, as well as differences in the mode of fishing (Clark, 1992). The former period is characterized by the formation of relatively stable, dense aggregations of fish, whereas in the latter period the orange roughy are more dispersed and widely distributed (Clark, 1991a). Fishing in winter generally involves shorter tows, often with smaller nets, than does out-of-season fishing.

[2] Francis, C., MAF Fisheries, pers. commun. 1991

In the following text, three colloquial area names have been used. These are given below with specific strata numbers (see Fig. 2):

Central Flat	strata 1, 4
Pinnacles	stratum 10
Westpac Bank	strata 9, 11

Results

Distribution

Trawl surveys The distribution of orange roughy in the survey area changed substantially between years (Fig. 3). In 1984 high catch rates were observed across much of the Central Flat area. (No trawls were made on the Pinnacles although heavy marks were observed on the echosounder; the survey did not cover the Westpac Bank area.) In 1987 fish were still widely distributed in the Central Flat; there were two main schools and further concentrations around the Pinnacles and the Westpac Bank. In 1988 there was a marked contraction in the area of high catch rates; a single small aggregation was observed on the Central Flat, and by 1989 there were no aggregations in the Central Flat region. High catch rates still occurred on the Pinnacles and Westpac Bank in 1989, and these actually increased in 1990, after the TAC and fishing effort were greatly reduced.

Commercial fishery The commercial fishery has been centered mainly inside the EEZ, targeting aggregations of orange roughy on the Central Flat and Pinnacles. Distribution of effort (number of tows) and catch between these two areas has changed over time (Table 3). In the period 1982–87, over 80% of the catch from the two areas was taken from the Central Flat with over 75% of the number of tows. In 1988 there was a marked increase in the proportion of catch and effort on the Pinnacles, and a corresponding reduction on the Central Flat. This shift continued in 1989 and 1990, during which the Pinnacles accounted for 65–70% of the catch. These changes reflect the change in distribution observed in the research trawl surveys.

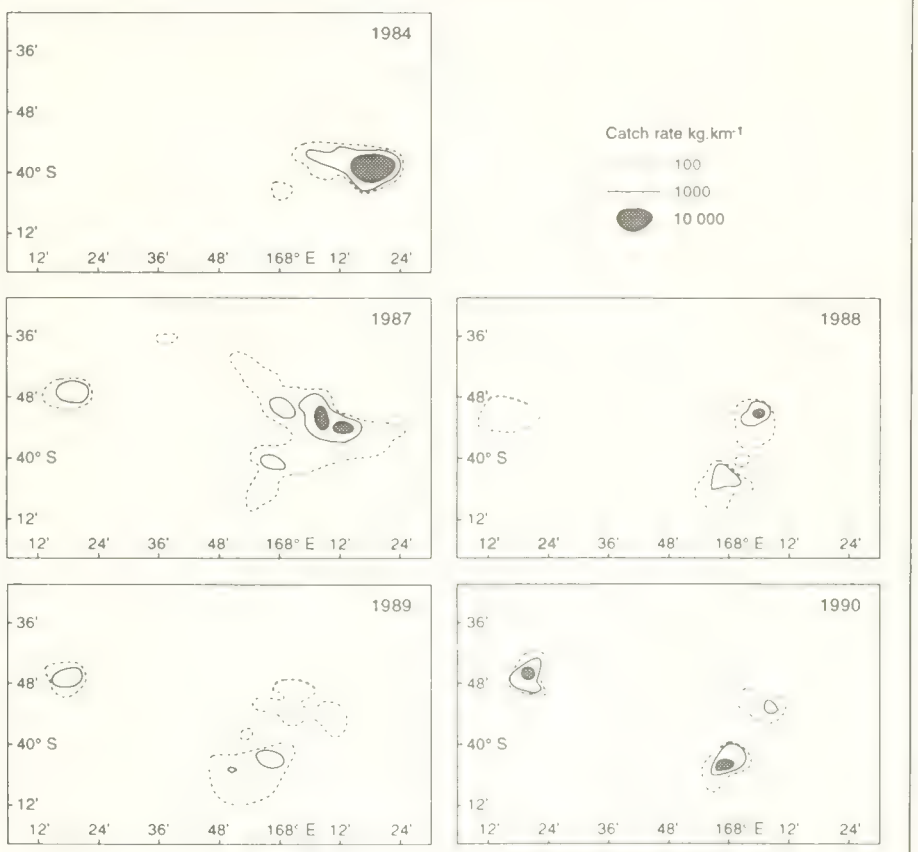

Figure 3
Contours of trawl survey catch rates (kg·km^{-1}) of orange roughy (*Hoplostethus atlanticus*) in 1984 and 1987–90.

Relative abundance

Trawl surveys Biomass indices (estimates of relative biomass) from trawl surveys in 1987, 1988, and 1989 are given in Table 4. The indices indicate a marked decline in biomass over the period. The distribution of biomass among strata changed over the years 1987–90 (Table 5). In 1987 and 1988 over 60% of the biomass was in the Central Flat area, but only 30% in 1989 and 1990. Over this period, there was an increase in the proportion on the Pinnacles, especially between 1989 and 1990. Biomass levels in the surrounding areas have fluctuated but were particularly high in 1989. The proportion of biomass on the Westpac Bank has remained comparatively constant.

Commercial fishery Mean catch per tow for all New Zealand vessels in the fishery from 1983 to 1991 is given in Table 6. Catch rates in winter, when the fish are aggregated for spawning, are generally higher than in other months. Although aggregations occur at other times, presumably for feeding, they are not as large or as stable as in winter. Catch rates in both periods declined steadily from 1983 to 1989 to between about 15% and 20% of original levels. The trend is slightly different in the two periods; winter catch rates declined more sharply to 1988, whereas in the other months the largest decrease was between 1983 and 1984. Catch rates increased in 1990, following a reduction of the TAC, when there were less vessels and fewer trawls on the grounds.

Individual trawl catch rates for orange roughy can be highly variable, consisting of 'hits' and 'misses.' Therefore it is not useful to describe the variance around these mean catch rates, beyond commenting that there is wide variation. It should be stressed that the changes in catch rates presented here may give an indication of changes in stock size but should be treated with caution. Difficulties in interpretation of such data for orange roughy are described in the 'Methods' section, and the form of relationship between mean catch per tow and stock abundance is uncertain.

Table 3

Distribution of commercial catch (% of total catch taken in the two areas) and effort (% of number of tows) for orange roughy (*Hoplostethus atlanticus*) for the Central Flat and Pinnacles (winter period, June to August).

	Central Flat		Pinnacles	
Year	% catch	% tows	% catch	% tows
1982	97.2	95.6	2.8	4.4
1983	97.0	94.7	3.0	5.3
1984	95.2	93.6	4.8	6.4
1985	87.7	78.0	12.3	22.0
1986	87.3	83.2	12.7	16.8
1987	84.4	77.3	15.6	22.7
1988	52.9	56.0	47.1	44.0
1989	34.0	43.3	66.0	56.7
1990	30.2	45.0	69.8	55.0

Table 4

Biomass indices (t) of orange roughy (*Hoplostethus atlanticus*) from trawl surveys, conducted from 1987 to 1989. (CV = coefficient of variation.)

Year	Biomass (t)	CV
1987	78,661	26
1988	30,946	27
1989	11,746	11

Stock reduction results

Abundance indices used in, and estimates of virgin biomass from, the stock reduction analyses are given in Table 7. Point estimates of B_0 range from 95,000 t to 278,000 t. The best fits of data to the model (those with the lowest CV) are from the winter CPUE series. Results from trawl survey data have higher CVs but confirm that an estimate of the order of 100,000 t is reasonable.

The 1987–89 trawl survey series gave the lowest virgin biomass estimate. It was not considered reliable because there were only three indices, and high fishing mortality rates were required to support the catch history. A maximum F of 1.0 is regarded as realistic for orange roughy (Francis et al., 1992). This constrains the virgin biomass to a minimum value of 94,000 t.

The estimate from non-winter CPUE is comparatively high. It has a large CV and is based on relatively low numbers of trawls (because most fishing effort is in winter). Such a biomass level would also

Table 5

Comparison of biomass estimates (t) of orange roughy (*Hoplostethus atlanticus*) by region from 1987 to 1990.

	1987		1988		1989		1990	
Region	Biomass (t)	%	Biomass (t)	%	Biomass (t)	%	Biomass (t)	%
Central Flat	56,636	72.0	21,051	68.0	3,275	27.9	4,228	30.8
Pinnacles	7,794	9.9	5,215	16.9	2,821	24.0	5,508	40.1
Surrounding background	10,717	13.6	2,878	9.3	5,088	43.3	3,208	23.3
Westpac Bank	3,514	4.5	1,802	5.8	563	4.8	794	5.8
Total	78,661	100.0	30,946	100.0	11,747	100.0	13,738	100.0

Table 6

Catch per unit of effort (mean catch (t) per trawl) of orange roughy (*Hoplostethus atlanticus*) for New Zealand fishing vessels.

Calendar year	Winter		Other months	
	CPUE	No. trawls	CPUE	No. trawls
1983	16.2	222	9.2	307
1984	15.3	54	5.2	515
1985	13.3	87	4.6	530
1986	10.5	512	3.3	486
1987	10.2	681	2.4	255
1988	5.9	1,269	2.7	99
1989	3.7	1,094	1.3	81
1990	6.6	325	7.3	25
1991	4.1	264	0.1	4

suggest low values of F in recent years, which seems unlikely given the substantial effort in the fishery yet catches being less than the TAC.

There is considerable uncertainty in all the data sets. However, assuming a virgin biomass of 110,000 t (as an approximation of the trawl survey and winter CPUE values), the decline in mid-year biomass of the population was rapid and the level in 1991 was about 20% of the virgin level (Table 8).

Other species

Biomass indices of the 12 main bycatch species caught in the trawl surveys from 1987 to 1989 are presented in Table 9. The coefficients of variation of these mean values range from 11% to 69% and differ between years and species, which limits their comparability.

However, there were no strong indications of increasing abundance of any species relative to abundance in 1987. There was little apparent change in abundance of ribaldo (*Mora moro*), leafscaled gulper shark (*Centrophorus squamosus*), widenosed chimaera (*Rhinochimaera pacifica*), spiky oreo (*Neocyttus rhomboidalis*), Owston's spiny dogfish (*Centroscymnus owstoni*), or white rattail (*Trachyrinchus* sp.). Declining abundance was suggested for big scaled brown slickhead (*Alepocephalus* sp.), basketwork eel (*Diastobranchus capensis*), Johnson's cod (*Halargyreus johnsoni*), smallscaled brown slickhead (*Alepocephalus australis*), shovelnosed spiny dogfish (*Deania calcea*), and seal shark (*Dalatias licha*). The biomass of species relative to orange roughy has generally increased for all species except seal shark. This change is strongest for ribaldo, Owston's dogfish, widenosed chimaera, leafscaled gulper shark, and white rattail.

Size structure

Length-frequency distributions of orange roughy from the entire survey area were similar in all years with no marked differences from the overall weighted length frequency (Fig. 4). There was a strong unimodal distribution with the peak at 32–33 cm standard length. Fish ranged in standard length from 9 cm to 44 cm.

Sex ratios varied between years, but were generally about 1 : 1. However, females always dominated the size distribution above about 35 cm. The mean

Table 7

Summary of biomass indices for orange roughy (*Hoplostethus atlanticus*) used in stock reduction analyses, and estimates of virgin biomass (B_0) (mean and 95% confidence interval), and coefficients of variation (CV).

Year	CPUE (winter)	CPUE (winter)	CPUE (other months)	Trawl survey (full area)	Trawl survey (reduced area)
1983	16.2	16.2	9.2		
1984	15.3	15.3	5.2		143,500
1985	13.3	13.3	4.6		
1986	10.5	10.5	3.3		
1987	10.2	10.2	2.4	78,600	75,000
1988	5.9	5.9	2.7	30,900	28,900
1989	3.7	3.7	1.3	11,700	11,000
1990		6.6	7.3		12,900
1991		4.1	0.1		
Parameter estimates					
B_0 (t)	100,000	122,000	278,000	83,000	95,000
B_0 (95% CI)	94,000–156,000	94,000–224,000	216,000–500,000	94,000–181,000	94,000–194,000
CV (%)	8	22	76	27	37

Table 8

Estimated biomass values by year (mid-year biomass, rounded to nearest 100 t) for orange roughy (*Hoplostethus atlanticus*).

Year	Biomass (t)	Year	Biomass (t)
1980	110,000	1986	67,000
1981	110,000	1987	54,900
1982	107,000	1988	40,500
1983	96,500	1989	28,400
1984	83,200	1990	22,300
1985	74,600	1991	21,400

size of females was significantly greater than that of males (t–test, $P<0.05$). Size data were also examined by the following subareas: Central Flat, Pinnacles, and Westpac Bank. Length frequencies by sex were generally similar to those for the total survey area and are not presented here. However, the distributions were approximately normal in shape and could be described by their means and standard errors to provide a simpler comparison between areas and between years (Fig. 5). There were no apparent differences between years or between areas (t–test, $P<0.05$), and no consistent trend in size over time.

Reproduction

All trawl surveys occurred during the months of June–July. There was considerable variation evident in the overall proportions of fish of different reproductive stage between years and areas (Table 10). To a large extent this reflected the timing of the survey (e.g. 1987 was earlier than the others) and showed a high proportion of maturing fish. However, in all years the majority of fish sampled were mature and were involved in that year's spawning (stages 3–6).

The Central Flat and Pinnacle regions were typically dominated by mature fish in or near spawning condition. In 1987 on the Westpac Bank there was a high proportion of fish that were in very early stages of maturation and hence unlikely to spawn in that year. From 1988 to 1990 the proportion of actively spawning fish increased. However, levels of nonspawning fish have consistently been higher here than in the Central Flat and Pinnacle areas.

Timing of spawning

The progression of gonad stages appeared consistent between years for which data spanning several weeks in July exist (Fig. 6). A pattern of maturing fish declining to low levels was observed early in

Table 9

Biomass (t) of the main bycatch species in the trawl surveys, their proportion of that year's orange roughy (*Hoplostethus atlanticus*) biomass (ref ORH), and their proportion of their biomass in 1987 (ref 1987).

	1987				1988				1989			
	Biomass	(CV)	Ref 1987	Ref ORH	Biomass	(CV)	Ref 1987	Ref ORH	Biomass	(CV)	Ref 1987	Ref ORH
Ribaldo	295	(14)	1.0	0.004	378	(16)	1.3	0.012	317	(11)	1.1	0.027
Owston's dogfish	567	(32)	1.0	0.007	358	(31)	0.6	0.011	400	(20)	0.7	0.034
Leafscaled gulper shark	160	(32)	1.0	0.002	167	(52)	1.0	0.005	208	(40)	1.3	0.018
Spiky oreo	75	(38)	1.0	0.001	156	(36)	2.1	0.005	68	(28)	0.9	0.006
Bigscaled brown slickhead	1,345	(20)	1.0	0.017	486	(21)	0.4	0.016	314	(20)	0.2	0.026
Basketwork eel	332	(19)	1.0	0.004	153	(37)	0.5	0.005	57	(39)	0.2	0.005
Johnson's cod	145	(17)	1.0	0.002	61	(36)	0.4	0.002	44	(16)	0.3	0.004
White rattail	467	(23)	1.0	0.006	345	(29)	0.7	0.011	610	(17)	1.3	0.052
Smallscaled brown slickhead	1,197	(39)	1.0	0.015	285	(22)	0.2	0.009	610	(13)	0.5	0.052
Widenosed chimaera	274	(21)	1.0	0.003	662	(20)	2.4	0.021	283	(16)	1.0	0.024
Shovelnosed dogfish	277	(23)	1.0	0.003	218	(41)	0.8	0.007	73	(31)	0.3	0.006
Seal shark	467	(32)	1.0	0.006	87	(69)	0.2	0.003	47	(39)	0.1	0.004

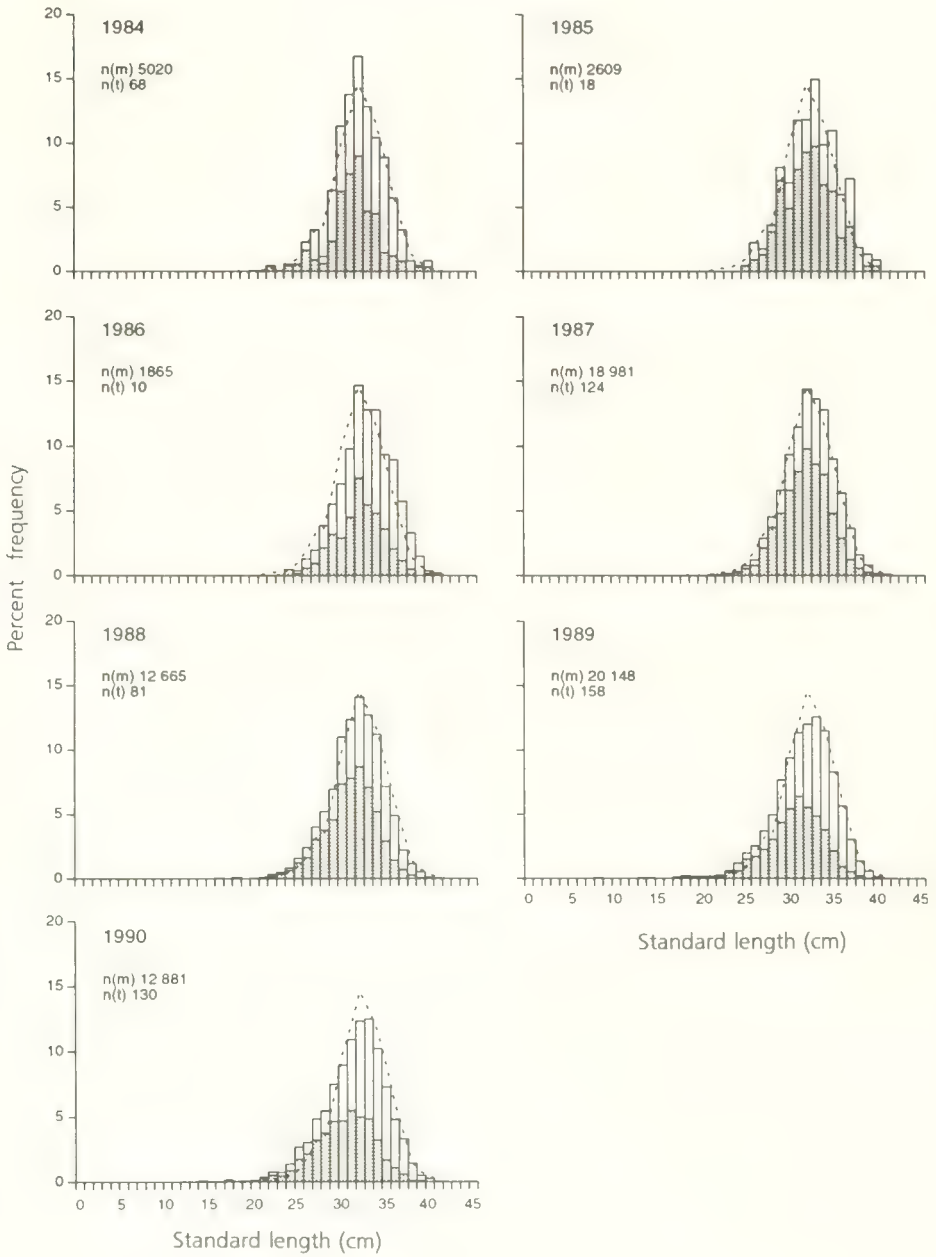

Figure 4

Length-frequency distribution of the orange roughy (*Hoplostethus atlanticus*) population by year (stipple=male, clear=female, dashed line=weighted length frequency for all years combined, $n(m)$=number of fish measured, $n(t)$=number of trawls from which samples were taken, data are scaled by stratum areas to represent total population-size distribution).

July; ripe fish dominated through mid-July; and the proportion of spent fish increased progressively from low levels during the first two weeks in July to peak in the third or fourth week.

Data are insufficient to examine regional variation in this pattern, but there may be some differences between areas; fish appear to spawn slightly later on the Westpac Bank than those on the Central

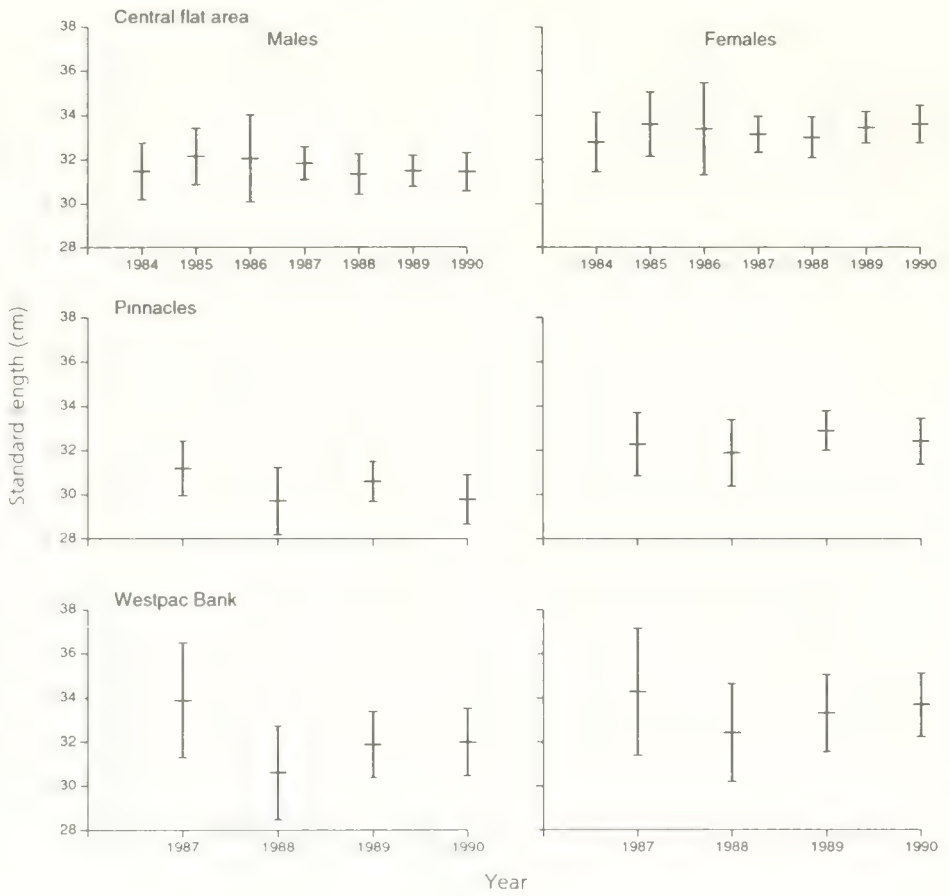

Figure 5

Mean length (±2 standard errors) of orange roughy (*Hoplostethus atlanticus*) by year in the three main spawning areas: Central Flat, Pinnacles, and Westpac Bank.

Flat and Pinnacles. The increase in ripe fish towards the end of the 1990 survey was due largely to sampling the Westpac Bank at this time.

The onset of spawning, defined as the first date on which 20% of fish sampled were spent (after Pankhurst, 1988), has been relatively consistent over the years (Table 11). Actual dates based on females have ranged from 9 July to 16 July.

Size at maturity

Mean lengths at maturity for males and females by year are given in Table 12. There is a significant trend of decreasing mean size for males (linear regression F–test, $P<0.05$), but there is no consistent trend for females.

Feeding

Data on frequency of occurrence of broad taxonomic prey groups from 1984 to 1990 showed the most common prey were natant decapod crustaceans and fish (Table 13).

The main groups that could be identified were macrourids (small species of *Coelorinchus* and *Coryphaenoides*) and myctophids (species of *Lampanyctus* and *Lampanyctodes*). Natant decapod crustacean prey were mainly species in the genera *Pasiphaea*, *Sergestes*, *Oplophorus*, and *Acanthephyra*. Squids and amphipods were also frequent prey.

Discussion

Orange roughy on the Challenger Plateau were overexploited in the late 1980s. Research trawl survey and commercial catch and effort data show similar changes in distribution and abundance. There was a marked contraction in the area of high catch rates,

Table 10

Gonad stage proportions of female orange roughy (*Hoplostethus atlanticus*) by area by year (n = sample size; 1 = immature/resting, 2 = early maturation, 3 = maturation, 4 = ripe, 5 = running ripe, 6 = spent).

	Gonad stage						
Area and year	1	2	3	4	5	6	n
Central Flat							
1987	0	2.8	81.9	14.7	0	0.6	531
1988	0	1.2	3.4	20.3	17.1	58.0	438
1989	0.3	1.2	20.5	46.5	12.4	19.1	591
1990	0.4	2.0	13.3	41.1	10.0	33.2	460
Pinnacles							
1987	0.4	8.5	74.4	15.9	0	0.8	246
1988	0	5.0	9.9	31.5	14.0	39.6	222
1989	0	1.6	17.6	43.4	7.3	30.1	426
1990	0.3	1.6	10.8	34.9	9.0	43.4	378
Westpac Bank							
1987	0	45.6	50.9	0	0	3.5	57
1988	0	33.7	16.3	32.6	2.3	15.1	86
1989	0	21.4	19.1	35.7	9.5	14.3	84
1990	3.9	15.1	17.5	35.9	8.7	18.9	206

Table 11

Date at which 20% of orange roughy (*Hoplostethus atlanticus*) sampled were spent.

Year	Male	Female
1984	13 July	12 July
1985	8 July	9 July
1986	after 16 July	10 July
1987	before 12 July	10 July
1988	10 July	16 July
1989	20 July	15 July
1990	11 July	9 July

Table 12

Mean length (cm) at maturity and two standard errors (SE), of orange roughy (*Hoplostethus atlanticus*) by sex and year.

	Male		Female	
Year	Length	2 SE	Length	2 SE
1984	27.1	0.54	25.7	0.68
1987	24.4	0.80	24.3	1.02
1988	23.2	1.12	22.7	1.56
1989	23.6	1.16	23.4	1.38
1990	22.3	1.10	24.5	1.00

a reduction in the number of spawning schools, and a marked decline in biomass. Stock reduction analyses have estimated virgin biomass to be about 110,000 t. The stock had declined to about 20% of this by 1991, well below the optimal long-term biomass of 30% of virgin levels predicted by computer modelling under an $F_{0.1}$ fishing strategy (Clark, 1992).

It is clear that the Challenger Plateau spawning population declined rapidly and substantially with commercial fishing in the 1980s. However, it is uncertain exactly how much of the change was directly attributable to the fishery. There are no data on size of the stock prior to its exploitation, so the level of any natural fluctuations in population size and distribution is unknown. It is possible that stock size might have decreased in the absence of any fishing, but it seems very unlikely, given the longevity of orange roughy, that such changes would occur as rapidly as we observed. There could also have been a progressive change in the availability of fish in the area covered by the trawl surveys or bulk of the commercial fleet. Adult orange roughy do not necessarily spawn each year (e.g. Bell et al., 1992; authors' unpubl. data) and hence may not migrate to the general spawning area. In the early years of the fishery, large catches were taken over much of the year, but the period of large catches became progressively reduced to the winter months (Clark, 1991a). This suggests that initially there were resident fish on the grounds, with a migratory component which used the area for spawning only. If this latter group had a variable number of spawners each year, this could have affected how well trawl survey or CPUE data reflected true biomass. However, if this occurred, greater variation in abundance indices between years than observed would be expected. There could also have been other spawning grounds that fish from the 'Challenger stock' used. However, there were no indications of this from either commercial or research survey trawling beyond the main grounds. A further alternative explanation for the observed decline in abundance could be a change in vulnerability to the trawl gear, either by fish residing above the bottom in midwater, or by heavy fishing pressure disrupting existing aggregations or preventing their formation. There is no information on the former (although no fish marks were noted on the echosounder above the bottom during the last two research surveys), but the latter is likely to have occurred (Clark and Tracey, 1991). The effects of fishing on school stability could have resulted in a greater decline in catch rates than true abundance, but reduced stability of schools

was not observed prior to 1988, and so does not explain the consistent downward trend in CPUE indices. Hence, although alternative hypotheses cannot be discounted, fishing is most likely to have been the major factor in the observed depletion of the stock.

Most other 'bycatch' species also declined in abundance, although changes were relatively minor compared with that of orange roughy. There was no strong indication of any 'species replacement' of orange roughy. The fishery on the Challenger Plateau targets specifically orange roughy, and other species are not caught in large quantities. In the trawl surveys, orange roughy have generally accounted for over 95% of the biomass. The commercial fishery would probably take even less bycatch than the surveys because it focuses on the aggregations which are usually almost exclusively orange roughy. Intuitively, some compensatory increase in other components of the Challenger Plateau community is to be expected because of the extent of orange roughy depletion, but there is no information on biomass, trophic interactions, and productivity of other fish or invertebrate species. In addition, even if most of the other finfish species have higher fecundity and faster growth rates than orange roughy, there could be a relatively long response time to changes in species dominance.

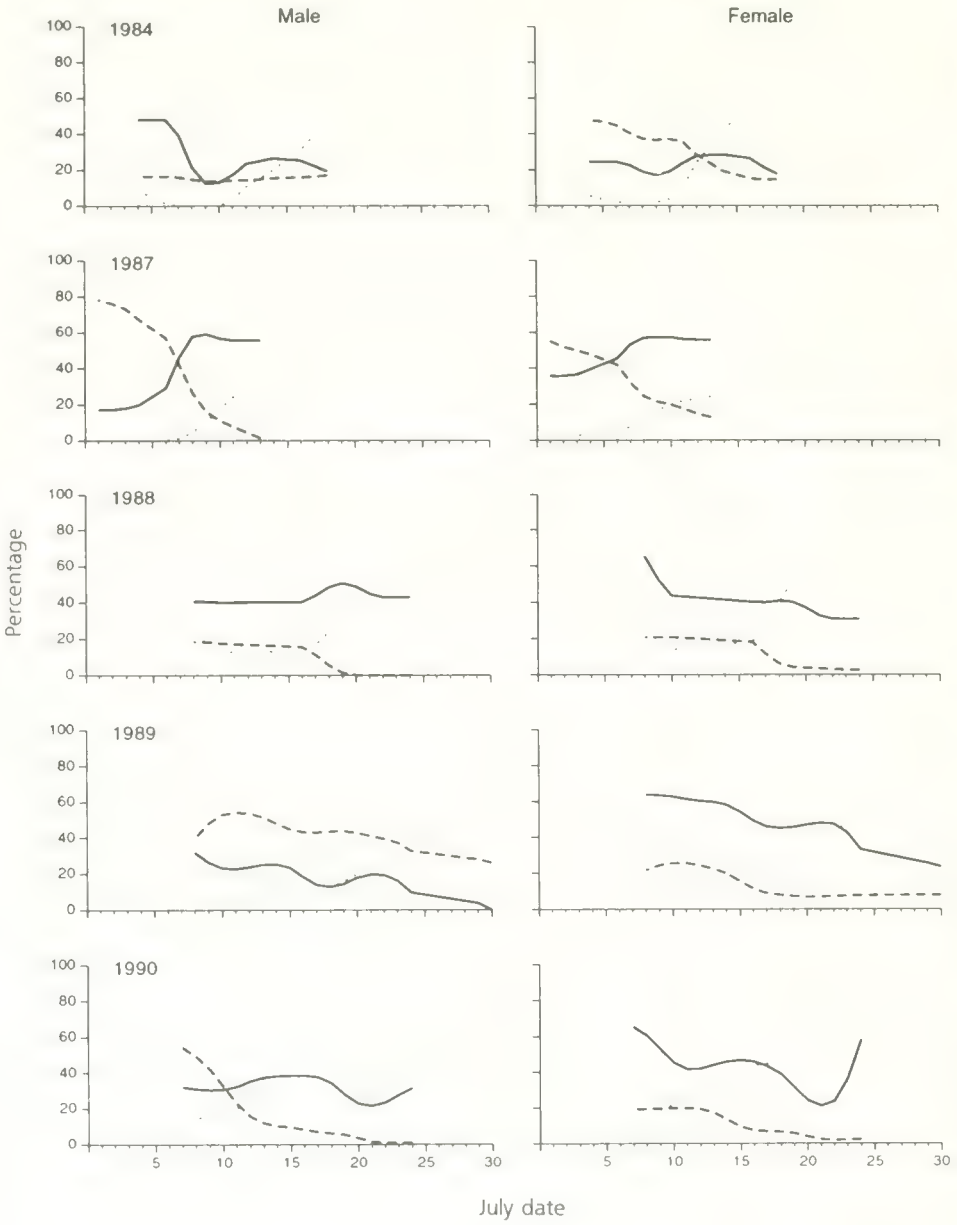

Figure 6

Relative proportions of maturing, ripe, and spent gonads of orange roughy (*Hoplostethus atlanticus*) by day during research surveys in 1984 and 1987–90 (5 day running mean; maturing=dashed line, ripe=solid line, spent=dotted line; maturing=stage-3 male, stage-3 female; ripe=stage-4 male, stages 4 and 5 female; spent=stage-5 male, stage-6 female).

There has been no apparent change in the size structure of the orange roughy population. With heavy exploitation, a truncation of the length frequency distribution and a reduction in the mean size of fish in the population might have been expected, as larger fish were removed and new recruits entered the population. Such changes in size structure of exploited populations are well documented (e.g.

Table 13

Frequency of occurrence of major prey groups of orange roughy (*Hoplostethus atlanticus*) by year.

	1984	1985	1986	1987	1988	1989	1990
Crustacea							
Amphipoda	13.5	7.6	0	6.3	8.0	19.1	5.9
Decapoda/Natantia	53.8	56.1	22.8	44.5	43.0	23.5	34.5
Euphausiacea/Mysidacea	4.3	0.7	13.6	7.7	8.0	2.8	2.3
Crustacean remains/other groups	6.4	5.3	9.1	13.5	9.3	10.0	9.3
Mollusca							
Cephalopoda	14.5	9.1	13.6	10.4	10.6	9.5	7.7
Thaliacea							
Salpidae	—			—	0.3	0.4	0.7
Teleosts	45.7	29.5	40.9	33.1	30.1	36.3	36.6

Smith, 1968; Gulland 1971; Edwards and Bowman, 1979; Grosslein et al., 1980; Rowling, 1990), although none of these studies have dealt with a species as long-lived or slow-growing as orange roughy. The length frequency distribution of spawning orange roughy consists largely of 25–40 cm fish. These sizes are probably fully vulnerable to trawl gear with 100 mm mesh size (legal minimum). Hence, there could be relatively constant fishing mortality across all size groups. There have been no indications of large numbers of new recruits in the length frequency data. This may suggest low levels of recruitment, or at least no entry of any strong year class since 1984 that would reduce mean size.

Interpretation of changes in size structure is also limited by the lack of age data for adult orange roughy. Available ageing data (Mace et al., 1990; MAF Fisheries[3]) for orange roughy suggest a wide range of ages for a given length, and it is possible that age structure may change more rapidly than size structure. Smith et al. (1991) reported a reduction in genetic diversity of orange roughy from several New Zealand areas, including the Challenger Plateau, and suggested this was due to higher mortality of older fish that may remain longer on the spawning grounds than that of younger fish.

Size at maturity showed a significant decline in males, but not in females. It is possible that one sex could be more vulnerable to fishing, but there are no indications of unbalanced sex ratios in commercial catches (authors' unpubl. data). Macroscopic examination of gonads for identification of gonad stage is more reliable in females, where criteria based on colour and size of oocytes are clearer than the presence of milt in male gonads. However, the data may not be representative of true size at maturity in the total population. It is possible that the size at maturity measured here is lower than the true population value because fish that migrate to the spawning grounds are primarily those that are mature, and the relative proportions of immature and mature small fish are not accurately represented.

The apparent lack of change in size at maturity is not surprising in view of the stability of the total population length frequency. An increase in growth rate, with a corresponding reduction in the age at maturity, of individuals in an exploited population is well documented (e.g. Pitt, 1975; Spangler et al., 1977; Borisov, 1978; Hempel, 1978; Leaman, 1991). However, Pitt (plaice, *Hippoglossoides platessoides,* on the Grand Banks) and Leaman (*Sebastes* spp. in the north Pacific Ocean) noted that whereas age at first maturity decreased with exploitation, size at maturity remained the same. Orange roughy are estimated to be about 24 years of age at maturity (Mace et al., 1990), and hence such functional changes in growth rate or maturity may not be obvious after 10 years of fishing, despite a major reduction in population size.

Orange roughy on the Challenger Plateau have consistently spawned in the same general area at the same time of year from 1984 to 1990. The gonad-stage pattern observed in trawl surveys has been similar each year. However, there is evidence of some regional variability in the proportion of fish spawning. The Central Flat and Pinnacles have consistently sustained levels of spawning fish over 90%. On the Westpac Bank this proportion has been lower, and the percentage spawning has progressively increased from 1987 (54%) to 1990 (81%). Reasons for this are not clear. Sample sizes from the Westpac Bank are smaller than those from the other areas but still come from at least six trawls, which should give a representative sample. In 1987 no

[3] MAF Fisheries, unpubl. data, 1993.

actively spawning fish were caught, perhaps because the survey had been taken in June/early July and peak spawning on the Westpac Bank could have occurred slightly later than in the other two areas (Clark, 1991b). Originally it was thought that fish on the Westpac Bank migrated east to the Central Flat and Pinnacles for spawning (Clark and Tracey, 1988). However, in subsequent years ripe and running-ripe fish were found. Nevertheless, in 1987 there was a large proportion of fish that were not spawning that year. It is possible that the Westpac Bank has only developed as a spawning ground since 1987, but if so, whether heavy fishing on the other grounds was a factor is unknown. The biomass index on the Westpac Bank has declined since 1987, so it is unlikely that there has been a major shift of fish from the Central Flat or Pinnacles.

The time of spawning (defined by 20% spent) has consistently been in the second and third weeks of July. Pankhurst (1988) reported that day length was a critical factor in synchronizing the reproductive cycle of orange roughy. The changes in dates of 20% spent between years do not correlate exactly with annual changes in the shortest day, but day length could nevertheless be an important general cue. Gonadal development has remained consistent despite major changes in the size of the population and the spawning school structure. There are indications that heavy fishing pressure may disrupt the stability of schools of orange roughy (Clark and Tracey, 1991). In 1989 when fishing effort was at its peak, a comparatively high proportion of the biomass was in 'background' areas, outside the three main regions of spawning activity. Catch rates in the spawning areas were lower than in other years. It is possible that fishing pressure was affecting the formation of aggregations, but nevertheless reproductive development still occurred normally. However, the success of spawning could have been reduced because the fish were more dispersed.

The diet of orange roughy, and the relative frequency of occurrence of prey groups, were similar over the period examined. Natant decapod crustaceans and fish remains have dominated the diet. This diet composition concurs with other accounts of orange roughy feeding habits in New Zealand waters (e.g. Liwoch and Linkowski 1986; Rosecchi et al., 1988) and is similar to diet composition of orange roughy in the North Atlantic Ocean (e.g. Mauchline and Gordon, 1984; Gordon and Duncan, 1987), Indian Ocean (Kotlyar and Lipskaya, 1981), and off southeastern Australia (Bulman and Koslow, 1992). The trophic effects of the decline in orange roughy biomass are unknown. There is little information on predator–prey relationships within communities containing orange roughy. Published feeding studies and observations from research cruises at different times during the year (authors' unpubl. data) indicate that orange roughy do not prey on eggs or larvae of other fish species. The only published data on predation of orange roughy record them in stomachs of seal shark on the Challenger Plateau (Clark and Tracey, 1988). Sperm whales (*Physeter catodon*) are often observed in orange roughy spawning areas, and although they can dive to depths of over 1000 m. It is uncertain whether they feed on orange roughy.

Orange roughy are slow-growing and long-lived with low productivity, making them highly susceptible to the effects of overfishing. Long-term sustainable yield for the Challenger Plateau stock is estimated at 1.6% of virgin biomass (Clark, 1992). In the early years of a developing fishery catch levels are likely to be high. The schooling behavior of orange roughy for spawning or feeding means that large catches can be taken in a short time, and high catch rates may be maintained despite decreasing biomass. CPUE declined on the Challenger Plateau but not as consistently on the Chatham Rise where the population was also reduced by heavy fishing (Francis et al., 1992), although there was a progressive shortening of the period over which high catch rates occurred (Coburn and Doonan, in press).

In 1986, the TAC on the Challenger Plateau was increased from 6,000 to 10,000 t in order to assess the impact of heavier fishing and to learn more about the productivity of orange roughy. At that stage there was little understanding of stock size, or age and growth characteristics of the species. Hence the intention was to increase catch sufficiently to provide a contrast in abundance indices and give information on the resilience of the stock. However, there were several problems with this 'adaptive management' strategy as applied to Challenger Plateau orange roughy. The first was that it began without good data on the abundance of the stock against which to measure any change. It would have been preferable to have had at least two years of abundance data before increasing fishing pressure. At the time, CPUE had not been examined, and trawl survey results were inadequate to estimate biomass. A new time series of trawl surveys began in 1987, and although the 1988 survey showed a large decrease, with only two survey results we could not be confident about interpreting the differences as a strong decline in stock size. A further difficulty with such management is that with a slow-growing species like orange roughy, potential effects of any changes in spawning stock size on recruitment will not be evident for 20–25

years when the results of that year's spawning recruit to the fishery. Hence, until that time the fishery will be removing only accumulated adult stock and low levels of virgin stock recruitment. A third important feature of adaptive management is the understanding that it can involve high risk to a species like orange roughy. Changes in biomass could occur rapidly and any quota system and industry response must be flexible, so catch levels can be reduced rapidly.

The recovery of orange roughy from heavy fishing may be slow. Their fecundity is low at 20,000–30,000 eggs·kg^{-1} body weight (Pankhurst and Conroy, 1987; Clark and Tracey, 1991). There is no evidence of a marked change in fecundity of Challenger Plateau fish over the period 1987–90 (authors' unpubl. data), but Leaman (1991) reported reduced fecundity in exploited stocks of *Sebastes alutus*, rather than an increase which might have been expected. In addition, Leaman and Beamish (1984) suggested a possible correlation between longevity of a species and the period between strong year classes. Brown et al. (1983) noted that a reduction in population size of several species in the Georges Bank region to low levels (10–20% of peak abundance) was followed by less frequent occurrence of strong year classes.

High vulnerability to fishing and possible slow recovery from over-fishing are important for management of orange roughy fisheries. Data over a comparatively long time period are required to provide a basis for sound management of long-lived species (Leaman, 1991). It is clear with orange roughy on the Challenger Plateau that such species can be overfished in a much shorter time than that required for the desired data collection. Hence, development of an orange roughy fishery needs careful control from the outset. It is important that research occurs in advance of substantial fishing, so that baseline data on distribution, abundance, and biology are collected. The most commonly used techniques for stock assessment of orange roughy (trawl survey, acoustic survey, CPUE analysis) provide relative abundance indices, and therefore require several surveys before absolute biomass can be determined. Results of surveys in other areas, where the relation between survey indices and true biomass has been established, may be useful, but only if gear, bottom type, and fish distribution are similar. Egg production surveys have been carried out in both New Zealand and Australia, and may enable more rapid assessment in some localized areas. 'Adaptive management,' as discussed above, may be appropriate as an aid to estimate biomass by stock reduction methods, but it must be carried out with flexibility in order to change catch levels quickly. If development of the fishery is carefully regulated in the first few years while such data are collected, later management problems such as too many vessels involved in the fishery and the need to quickly and substantially decrease quota levels could be avoided.

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Literature cited

Bell, J. D., J. M. Lyle, C. M. Bulman, K. J. Graham, G. M. Newton, and D. C. Smith.
1992. Spatial variation in reproduction, and occurrence of non-reproductive adults, in orange roughy, *Hoplostethus atlanticus* Collett (Trachichthyidae), from southeastern Australia. J. Fish. Biol. 40:107–122.

Borisov, V. M.
1978. The selective effect of fishing on the population structure of species with a long life cycle. J. Ichthyol. 18:896–904.

Brown, B. E., V. C. Anthony, E. D. Anderson, R. C. Hennemuth, and K. Sherman.
1983. The dynamics of pelagic fishery resources off the northeastern coast of the United States under conditions of extreme fishing perturbations. *In* G. D. Sharp and J. Csirke (eds.), Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources. FAO Fish. Rep. 291:465–505.

Bulman, C. M., and J. A. Koslow.
1992. Diet and food composition of a deep-sea fish, orange roughy *Hoplostethus atlanticus* (Pisces: Trachichthyidae), off southeastern Australia. Mar. Ecol. Prog. Ser. 82:115–129.

Clark, M. R.
1991a. Commercial catch statistics for the orange roughy fishery on the Challenger Plateau, 1980–90. N.Z. Fish. Tech. Rep. 27, 11 p.
1991b. Orange roughy fisheries in the mid–Tasman Sea. *In* K. Abel, M. Williams, and P. Smith (eds.), Australian and New Zealand southern trawl fisheries conference. Aust. Bureau of Rural Resources Proc. 10:223–229.

1992. Assessment of the Challenger Plateau (ORH7A) orange roughy fishery for the 1992–93 fishing year. N.Z. Fish. Assess. Res. Doc. 92/6, 13 p. Avail. MAF Fisheries, P.O. Box 297, Wellington, N.Z.

Clark, M. R., and R. I. C. C. Francis.

1990. Revised assessment of the Challenger Plateau (QMA7A) orange roughy fishery for the 1989–90 fishing year. N.Z. Fish. Assess. Res. Doc. 90/1, 17 p. Avail. MAF Fisheries, P.O. Box 297, Wellington, N.Z.

Clark, M. R., and D. M. Tracey.

1988. Report of an orange roughy trawl survey on Challenger Plateau, June–July 1987. N.Z. Fish. Res. Cent. Int. Rep. 86, 87 p. Avail. MAF Fisheries, P.O. Box 297, Wellington, N.Z.

1991. Trawl survey of orange roughy on the Challenger Plateau, July 1990. N.Z. Fish. Tech. Rep. 26, 20 p.

Coburn, R. P., and I. J. Doonan.

In press. Orange roughy fishing on the North East Chatham Rise: a description of the commercial fishery, 1979–1988. N.Z. Fish. Tech. Rep.

Edwards, R. L., and R. E. Bowman.

1979. Food consumed by continental shelf fishes. *In* H. Clepper (ed.), Predator–prey systems in fisheries management, p. 387–405. Sport Fishing Inst., Washington, D.C.

Fenton, G. E., S. A. Short, and D. A. Ritz.

1991. Age determination of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae), using 210Pb : 226Ra disequilibria. Mar. Biol. 109:197–202.

Francis, R. I. C. C.

1981. Stratified random trawl surveys of deep-water demersal fish stocks around New Zealand. N.Z. Fish. Res. Div. Occas. Pub. 32, 28 p.

1984. An adaptive strategy for stratified random trawl surveys. N.Z. J. Mar. Freshwater Res. 18:59–71.

1990. A maximum likelihood stock reduction method. N.Z. Fish. Assess. Res. Doc. 90/4, 12 p. Avail. MAF Fisheries, P.O. Box 297, Wellington, N.Z.

1992. Use of risk analysis to assess fishery management strategies: a case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. Can. J. Fish. Aquat. Sci. 49: 922–930.

Francis, R. I. C. C., D. A. Robertson, M. R. Clark, and R. P. Coburn.

1992. Assessment of the ORH 3B orange roughy fishery for the 1992/93 fishing year. N.Z. Fish. Assess. Res. Doc. 92/4, 45 p. Avail. MAF Fisheries, P.O. Box 297, Wellington, N.Z.

Gordon, J. D. M., and J. A. R. Duncan.

1987. Aspects of the biology of *Hoplostethus atlanticus* and *H. mediterraneus* (Pisces: Berycomorphi) from the slopes of the Rockall Trough and the Porcupine Sea Bight (North-Eastern Atlantic). J. Mar. Biol. Ass. U.K. 67:119–133.

Grosslein, M. D., R. W. Langton, and M. P. Sissenwine.

1980. Recent fluctuations in pelagic fish stocks of the Northwest Atlantic, Georges Bank region, in relation to species interactions. Rapp. P.-v. Réun. Cons. int. Explor. Mer 177:374–404.

Gulland, J. A.

1971. Ecological aspects of fishery research. Adv. Ecol. Res. 7:115–176.

Gunderson, D. R.

1977. Population biology of Pacific ocean perch, *Sebastes alutus*, stocks in the Washington-Queen Charlotte Sound region, and their response to fishing. Fish. Bull. 75:369–403.

Hempel, G.

1978. North Sea fisheries and fish stocks: a review of recent changes. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:145–167.

Kotlyar, A. N., and N. Y. Lipskaya.

1981. Feeding of *Hoplostethus atlanticus* Collett (Trachichthyidae, Beryciformes). *In* Fishes of the open ocean, p. 89–93. Inst. Oceanology, Academy of Sciences USSR, Moscow.

Leaman, B. M.

1991. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. Env. Biol. Fish. 30:253–271.

Leaman, B. M., and R. J. Beamish.

1984. Ecological and management implications of longevity in some Northeast Pacific groundfishes. Int. North Pac. Fish. Comm. Bull. 42:85–97.

Liwoch, M., and T. B. Linkowski.

1986. Some biological features of orange roughy *Hoplostethus atlanticus* (Trachichthyidae) from New Zealand waters. Pr. morsk. Inst. ryb. Gdyni 21:27–41.

Mace, P. M., J. M. Fenaughty, R. P. Coburn, and I. J. Doonan.

1990. Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the north Chatham Rise. N.Z. J. Mar. Freshwater Res. 24:105–119.

Mauchline, J., and J. D. M. Gordon.

1984. Occurrence and feeding of berycomorphid and percomorphid teleost fish in the Rockall Trough. J. Cons. int. Explor. Mer 41:239–247.

Pankhurst, N. W.

1988. Spawning dynamics of orange roughy, *Hoplostethus atlanticus*, in mid-slope waters of New Zealand. Env. Biol. Fish. 21:101–116.

Pankhurst, N. W., and A. M. Conroy.

1987. Size-fecundity relationships in the orange roughy, *Hoplostethus atlanticus*. N.Z. J. Mar. Freshwater Res. 21:295–300.

Pankhurst, N. W., P. J. McMillan, and D. M. Tracey.

1987. Seasonal reproductive cycles in three commercially exploited fishes from the slope waters off New Zealand. J. Fish Biol. 30:193–212.

Pauly, D.

1979. Theory and management of tropical multi-

species stocks. A review, with emphasis on the Southeast Asian demersal fisheries. ICLARM Stud. Rev. 1.

Pearson, E. S., and H. O. Hartley (eds.).
1976. Biometrika tables for statisticians. 2 vols. Cambridge Univ. Press, Cambridge.

Pitt, T. K.
1975. Changes in abundance and certain biological characteriplatessoides.stics of Grand Bank American plaice, *Hippoglossoides platessoides*. J. Fish. Res. Board Can. 32:1383–1398.

Regier, H. A., and K. H. Loftus.
1972. Effects of fisheries exploitation on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29:959–968.

Robertson, D. A.
1991. The New Zealand orange roughy fishery: an overview. *In* K. Abel, M. Williams, and P. Smith (eds.), Australian and New Zealand southern trawl fisheries conference. Aust. Bureau of Rural Resources Proc. 10:38–48.

Rosecchi, E., D. M. Tracey, and W. R. Webber.
1988. Diet of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae) on the Challenger Plateau, New Zealand. Mar. Biol. 99:293–306.

Rowling, K. R.
1990. Changes in the stock composition and abundance of spawning gemfish *Rexea solandri* (Cuvier), Gempylidae, in southeastern Australian waters. Aust. J. Mar. Freshwater Res. 41:145–163.

Russ, G. R., and A. C. Alcala.
1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. Mar. Ecol. Prog. Ser. 56:13–27.

SAS.
1988. SAS/STAT Users Guide, Release 6.03 ed. SAS Institute, Cary, NC.

Smith, P. J., R. I. C. C. Francis, and M. McVeagh.
1991. Loss of genetic diversity due to fishing pressure. Fish. Res. 10:309–316.

Smith, S. H.
1968. Species succession and fishery exploitation in the Great Lakes. J. Fish. Res. Board Can. 25:667–693.

Spangler, G. R., N. R. Payne, J. E. Thorpe, J. M. Byrne, H. A. Regier, and W. J. Christie.
1977. Responses of percids to exploitation. J. Fish. Res. Board Can. 34:1983–1988.

Tracey, D. M., P. J. McMillan, J. H. Armstrong, and D. A. Banks.
1990. Orange roughy trawl survey: Challenger Plateau and west coast South Island, 1983. N.Z. Fish. Tech. Rep. 22, 34 p.

Morphometric and genetic identification of eggs of spring-spawning sciaenids in lower Chesapeake Bay*

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Abstract.—Restriction-fragment length polymorphism (RFLP) analysis of mitochondrial mtDNA was used to identify morphologically similar eggs of spring spawning sciaenids in lower Chesapeake Bay. During spring 1990 and 1991, ichthyoplankton surveys were conducted in lower Chesapeake Bay to estimate seasonal egg production and population biomass of black drum, *Pogonias cromis*. Rearing experiments indicated that at least three species of sciaenid (silver perch, *Bairdiella chrysoura*; weakfish, *Cynoscion regalis* and *P. cromis*) were spawning in the survey area during both years. Specific identification of eggs based on previously published ranges of outside egg diameter (OED) were not reliable because of considerable overlap in diameter distributions. However, analysis of weekly OED frequencies revealed the presence of three modes which differed in temporal occurrence, suggesting the products of three species. Genetic typing of eggs using RFLP analysis of mtDNA confirmed the presence of three species, but demonstrated that eggs of certain size classes represented two species. These results illustrate that reliance on previously published ranges of egg diameter for specific identification of spring-spawning sciaenids may overestimate the spawning biomass of black drum in Chesapeake Bay by as much as 50% owing to misidentification of weakfish eggs.

At least five species of the family Sciaenidae (silver perch, *Bairdiella chrysoura*; spotted seatrout, *Cynoscion nebulosus*; weakfish, *C. regalis*; northern kingfish, *Menticirrhus saxatilis*; and black drum, *Pogonias cromis*) are purported to spawn during the spring in lower Chesapeake Bay (Joseph et al., 1964; Lippson and Moran, 1974; Johnson, 1978; Brown, 1981; Olney, 1983; Cowan et al., 1992). The eggs of spring-spawning sciaenids in lower Chesapeake Bay are morphologically similar, ranging in outside egg diameter (OED) from 0.66 to 1.18 mm, and having single or multiple oil globules of varying sizes (Johnson, 1978; Olney, 1983). As a result, specific identification of eggs based on morphological criteria is problematic. Holt et al. (1988) suggested that it may not be possible to determine the specific identity of sciaenid eggs from morphological criteria; Joseph et al. (1964) reported that positive identification could only be achieved with supplemental hatching studies.

Hatching studies have traditionally been used to identify morphologically similar eggs, including those of sciaenids. Joseph et al. (1964) cultured eggs of several sciaenids collected at a single station in southern Chesapeake Bay (16 May 1962) and raised larvae to an identifiable size (5–7 mm). The smallest eggs (0.630–0.777 mm) were found to be *B. chrysoura*, whereas the larger eggs (0.814–1.110 mm) developed into *P. cromis*. Culture of eggs (0.777–0.950 mm) collected during early June produced no *P. cromis* but did result in larvae of *B. chrysoura* and *C. regalis*. In contrast, Olney (1983) suggested that eggs of *P. cromis*, *C. regalis*, *B. chrysoura*, and *Menticirrhus* spp. were included in a size-frequency distribution of morphologically similar eggs collected from May through August in lower Chesapeake Bay, but that identifications based on diameter were ambiguous because of the high degree of overlap in diameter distributions (Table 1). Confounding this problem is the observation that egg size may change with varying salinity or as the spawning season progresses (Johnson, 1978).

Because many species of Sciaenidae in lower Chesapeake Bay spawn concurrently and have morphologically similar eggs, most studies have relied either on previously published egg size distributions or rearing for identification (Holt et al., 1985, 1988; Comyns et

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Table 1

Reported range of outside egg diameter (OED) and study location for spring-spawning sciaenids.

Species	OED (mm)	Location	Author(s)
Bairdiella chrysoura	0.62–0.78	Chesapeake Bay	Joseph et al., 1964
	0.59–0.82	NW Gulf of Mexico	Holt et al., 1988
Cynoscion nebulosus	0.60–0.85	NW Gulf of Mexico	Holt et al., 1988
	0.70–0.85	NW Gulf of Mexico	Fable et al., 1978
Cynoscion regalis	0.68–1.18	Long Island Sound	Merriman and Sclar, 1952
	0.70–1.17	Chesapeake Bay	Pearson, 1929
	0.84–0.96	Delaware Bay	Wisner, 1965
Menticirrhus saxatilis	0.80–0.85	New Jersey	Welsh and Breeder, 1923
Menticirrhus spp.	0.63–0.87	NW Gulf of Mexico	Holt et al., 1988
Pogonias cromis	0.82–1.02	Chesapeake Bay	Joseph et al., 1964
	0.90–1.20	NW Gulf of Mexico	Holt et al., 1988

al., 1991; Saucier and Baltz, 1992; Saucier et al., 1992). However, the misidentifications that can result from overlapping egg-diameter distributions and the time-consuming nature of culture experiments make methods based on other characters desirable.

The application of biochemical genetics has provided an alternative to culture for positive identification of morphologically similar eggs. Electrophoresis of water-soluble proteins (allozyme analysis) has been used to distinguish between larvae and juveniles of morphologically similar species of marine fishes (eg. Morgan, 1975; Smith and Benson, 1980; Graves et al., 1988). Similarly, restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA has been employed to discriminate between the eggs of three congeneric serranids that could not be unambiguously identified with a single allozyme locus (Graves et al., 1990). More recently, direct sequencing and RFLP analysis of DNA amplified by the polymerase chain reaction (PCR) have been used to identify morphologically similar larvae of invertebrates (Olson et al., 1991; Silberman and Walsh, 1992).

In this paper we report that identification of eggs of sciaenids in lower Chesapeake Bay during spring based on published morphological criteria, rearing experiments, and genetic analysis are inconsistent. These results indicate that it is not possible to identify sciaenid eggs accurately by using diameter as the sole criteria. In addition, we present the results of weekly plots of egg size-frequency distributions and a RFLP analysis of mtDNA to determine the specific composition of eggs of sciaenids that may be present in lower Chesapeake Bay during spring.

Material and methods

Weekly zooplankton surveys of the lower Chesapeake Bay were conducted during April and May 1990 and 1991 to determine the distribution and abundance of eggs of black drum for an estimate of seasonal egg production. Samples of eggs were obtained with an *in situ* silhouette photography system consisting of paired 60-cm diameter, 335-μ nets fitted to a rigid frame (see Olney and Houde, 1993, for a detailed gear description). All deployments were 5-minute, stepped-oblique tows and yielded a standard plankton sample and a replicate film record. Plankton samples were preserved in 5–8% buffered formalin and sciaenid eggs were identified by using the criteria of Lippson and Moran (1974) and measured to the nearest 0.025 mm with a Zeiss Stemi SR stereomicroscope. Ten subsamples of eggs (n=75–100) sorted from preserved plankton samples were remeasured to assess measurement error.

During several cruises in May 1990 and 1991, eggs were collected in an area off the city of Cape Charles, Virginia, with a 0.5-m Hansen net fitted with 202-μ mesh to seed 1-liter Imhoff settling cones for hatching experiments. Eggs were originally separated as Type I (<0.80 mm) and Type II (>0.85 mm) based on the morphological criteria of Joseph et al. (1964). Rearing chambers were returned to the laboratory and held for 3 to 14 days. In these, larvae were periodically sac-

rificed and preserved in 5–8% buffered formalin. Identifications of preserved sciaenid larvae from pigment characters were based on Ditty (1989).

Sciaenid eggs collected in the same area during spring 1991, 1992, and 1993 were sorted from fresh plankton samples. To avoid contamination by the morphologically similar eggs of the cynoglossid *Symphurus plagiusa* and the soleid *Trinectes maculatus* that contain several oil globules and are abundant in lower Chesapeake Bay during the spring, all eggs with >3 oil globules were omitted from the samples. Although eggs of most spring-spawning sciaenids generally possess three or fewer oil globules (usually two) those of *Menticirrhus saxatilis* may contain from 1 to 16 oil globules (Johnson, 1978). After sorting, eggs were measured, placed in scintillation vials with 26 ppt seawater, and frozen at –70°C for genetic analysis. Individual eggs were thawed and remeasured prior to homogenization to assess shrinkage.

Sciaenid eggs were genetically typed by comparing mtDNA restriction fragment patterns of individual eggs with those of known adults. To obtain patterns of known adults, mature female sciaenids (*B.chrysoura*, *C. nebulosus*, *C. regalis*, *M. saxatilis*, and *P. cromis*) were collected by pound net, trawls, and hook and line in April and May 1990 and 1991. Ovarian tissue was excised and frozen at –70°C. MtDNA was purified from ovarian tissue by cesium chloride equilibrium density gradient ultracentrifugation following the protocols of Lansman et al. (1981). To determine a restriction enzyme that unambiguously identified the different sciaenid species, aliquots of mtDNA were individually digested with the following restriction enzymes: *Apa*I, *Ava*I, *Ban*I, *Ban*II, *Hin*dIII used according to manufacturer's instructions. The resulting fragments were separated electrophoretically on 1.0% agarose mini-gels run at 5 V/cm for four hours and visualized with ethidium bromide.

MtDNA-enriched genomic DNA was isolated from individual eggs following the protocols of Graves et al. (1990). Entire DNA samples were digested with a single discriminating restriction endonuclease, separated electrophoretically, and transferred to a nylon filter (Southern transfer) following standard protocols (Sambrook et al., 1989). Filters were hybridized with highly purified black drum mtDNA, nick-translated with biotin-7–dATP, washed, blocked and visualized following the methods of Graves et al. (1990).

Results

A total of 10,803 sciaenid eggs was sorted from samples collected in 1990 and 1991. Outside egg diameter of all specimens ranged from 0.650 to 1.12 mm. Successive blind readings of samples of 75 to 100 eggs were used to assess measurement error. No differences were found in the size-frequency distributions indicating good agreement within the 0.025–mm size classes (two-sample t-test, $P<0.05$, $n=79$).

Qualitative analysis of culture experiments using the two egg types of Joseph et al. (1964) revealed the presence of three species. Cultures containing eggs designated Type I (<0.80 mm) resulted in larvae of *B. chrysoura*, whereas cultures of eggs designated Type II (>0.85 mm) resulted in larvae of *C. regalis* and *P. cromis*.

Analysis of preserved ichthyoplankton samples from 1990 and 1991 revealed the presence of larvae of *B. chrysoura*, *C. regalis*, and *P. cromis*. No early life history stages of other sciaenids were identified; however, yolk-sac larvae could not be identified to species. Because rearing studies and analysis of field-caught plankton samples revealed the presence of more than two species, we could not rely on the criteria of Joseph et al. (1964) for specific identification. We therefore examined weekly frequency of occurrence of all sciaenid eggs during 1990 (Fig. 1) and 1991 (Fig. 2). Based on temporal occurrence and size frequency we identified three modes. The largest eggs (>0.975 mm), Type C, were most abundant during the period 23 April through 9 May. Type-C eggs declined in abundance throughout May in both years. Mid-sized eggs (0.850–0.950 mm), designated Type B, generally appeared later than Types A and C. Type-B eggs did not exceed 5% of the total frequency of sciaenid eggs until 15 May 1990 and 9 May 1991. Type-B eggs increased in abundance from mid-May until the end of sampling. The smallest eggs (<0.850 mm), designated Type A, co-occurred with Type-C eggs; however, they did not exceed 5% of the total sciaenid eggs until 8 May 1990 and 9 May 1991. In 1990, Type-A eggs peaked in abundance on 15 May and gradually declined throughout the sampling period. In 1991, Type-A eggs were most abundant during the last sample on 28 May.

To test the hypothesis that eggs designated Types A, B, and C were separate species assemblages, the mtDNA restriction fragment patterns of known adult sciaenids were compared with those of fresh egg samples separated into Types A, B, and C. Restriction fragment length polymorphism analysis of mtDNA, purified from adult *B. chrysoura*, *C. nebulosus*, *C. regalis*, *Menticirrhus saxatilis*, and *P. cromis*, revealed species-specific restriction fragment patterns for each of the five enzymes. Of the five enzymes, *Hin*dIII showed the greatest differences between species, facilitating visualization with the Southern blotting procedure (Table 2).

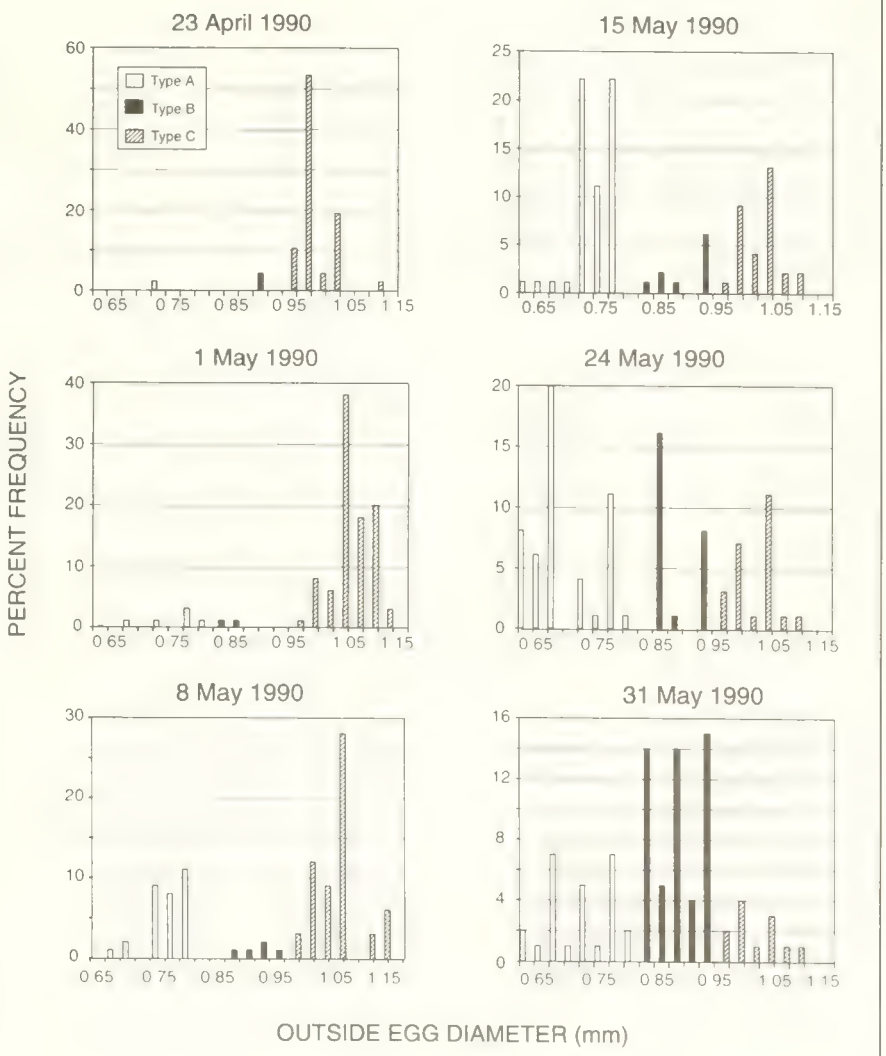

Figure 1

Frequency distributions of outside egg diameters of sciaenid eggs collected over six weeks during spring 1990 in lower Chesapeake Bay.

A total of 62 eggs, representing all sciaenid egg size classes collected in lower Chesapeake Bay, was identified with diagnostic *Hin*dIII restriction fragment patterns. *Bairdiella chrysoura*, *C. regalis*, and *P. cromis* were the only species of sciaenids identified; no other restriction fragment patterns were observed. Genetic identification of eggs designated Type A (<0.850 mm, n=12) resulted in 11 individuals of *B. chrysoura* and one specimen (0.825-mm OED size class) of *C. regalis* (Fig. 3). *Cynoscion regalis* composed the majority of type-B eggs (0.850-0.975 mm, n=18) analyzed, but seven of the 10 largest type-B eggs (0.975-mm OED size class) were identified as black drum. Type-C eggs, those 1.00 mm and larger (n=32), all possessed the restriction fragment pattern diagnostic for *P. cromis*.

Discussion

Identifications of eggs of sciaenids are often based on published diameter distributions or hatching experiments, or both. Results of hatching experiments and genetic analysis in this study indicate that samples of eggs of a single size class may represent the products of two or more species. For example, eggs designated Type I (<0.80 mm) and identified as silver perch by Joseph et al. (1964) were shown with genetic analysis to contain eggs of both weakfish and silver perch. Similarly, eggs designated Type II (>0.85 mm) and identified as black drum by Joseph et al. (1964) were shown with rearing and genetic analysis to contain eggs of both weakfish and black drum.

During the present study, neither hatching experiments nor genetic analysis identified eggs as black drum that were smaller than 0.975 mm OED. While temporally limited, the results of this study suggest that the range in size for eggs of black drum (0.975–1.125 mm) in lower Chesapeake Bay may be more restricted than those previously reported.

The ranges of egg diameter overlapped for silver perch and weakfish. Eggs genetically identified as silver perch ranged in size from 0.650 to 0.825 mm, in agreement with previously reported size ranges for silver perch in the northwestern Gulf of Mexico (0.59–0.82 mm, Holt et al., 1988) and Chesapeake Bay (0.625–0.775 mm, Joseph et al., 1964). Although Holt et al. (1988) identified eggs of silver perch as small as 0.590 mm, no sciaenid eggs smaller than 0.650 mm OED were collected in the present study. Sizes of eggs genetically identified as weakfish were found to range from 0.825 to 0.975 mm in diameter. These values are comparable with those reported by Wisner (1965, 0.84–0.96 mm) but are narrower than

the range (0.68–1.18 mm) given by Merriman and Sclar (1952) for Block Island Sound, New York. While the range in sizes for silver perch and weakfish reported in this study agree with past research, overlaps in these ranges preclude the sole use of egg size for identification.

Neither Joseph et al. (1964), Olney (1983), nor the present study identified eggs of *C. nebulosus* or *M. saxatilis* in samples collected in lower Chesapeake Bay. Fable et al. (1978) described laboratory-spawned eggs of *C. nebulosus* from a single female and reported a mean diameter of 0.77 mm (range 0.70–0.85 mm). Although based upon a limited sample size, Fable et al.'s data indicate that eggs of *C. nebulosus* could be confused with eggs of *B. chrysoura*; however, no eggs in our limited sample of this size range (n=12) were genetically identified as *C. nebulosus*. A possible explanation for the lack of eggs of *C. nebulosus* in the present study may be the tendency for adults to spawn in or around vegetated areas (Brown, 1981). The absence of eggs of *Menticirrhus* spp. in this genetic analysis may be explained by our exclusion of eggs with greater than three oil globules. Additionally, *Menticirrhus saxatilis* reportedly spawns off front beaches and possibly offshore (deSylva et al., 1962); consequently, circulation in the bay may prevent eggs of this species from entering the survey area or they may be transported to areas that were not sampled in our study.

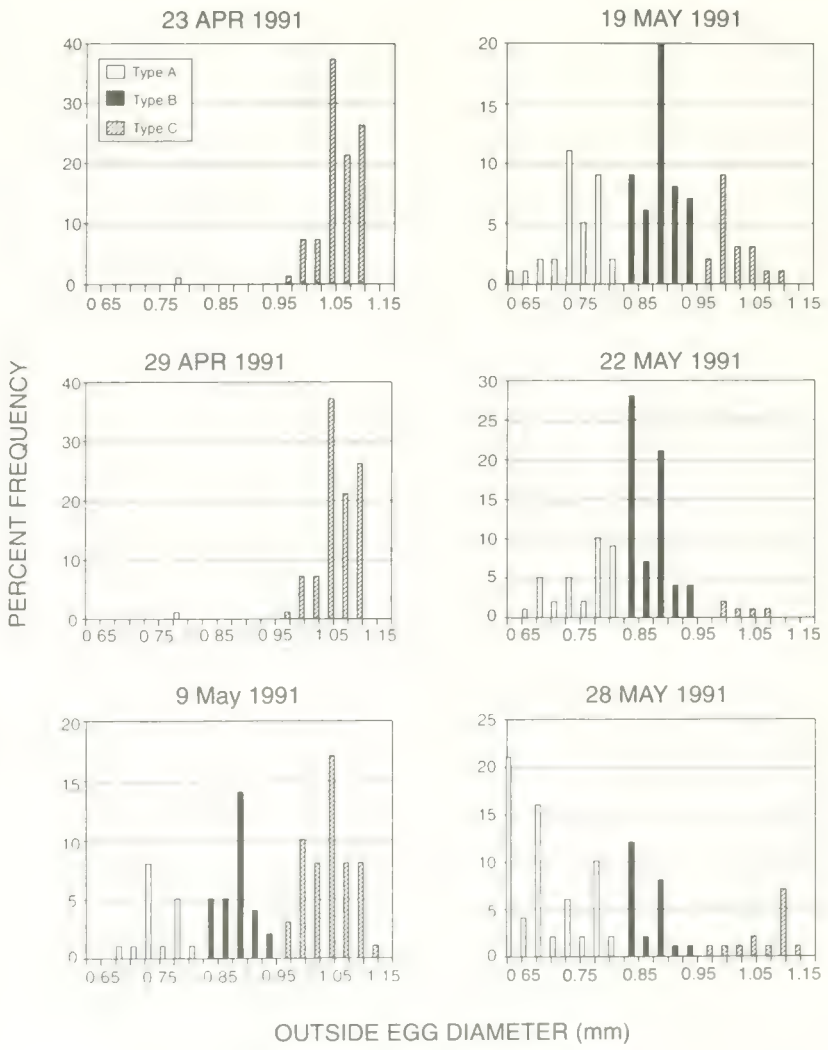

Figure 2

Frequency distributions of outside egg diameters of sciaenid eggs collected over six weeks during spring 1991 in lower Chesapeake Bay.

The identification of species-specific restriction fragment patterns for spring-spawning sciaenids is based on the assumption that there is limited intraspecific variation of the diagnostic restriction fragment patterns. Recent studies of the population genetics of spotted seatrout, black drum, and weakfish (Graves et al., 1992; Gold et al., 1993) indicate that these species exhibit low intraspecific mtDNA variability. Furthermore, no variation of the *Hin*dIII fragment pattern was found in a survey of mtDNA isolated from 25 adult *B. chrysoura* (L. Daniel, unpubl. data). Consequently, the common restriction fragment patterns used to distinguish species in this study were deemed suitable for use in identifications.

Variability in egg-size distributions with changing salinity and over the spawning season were not examined in this study. Consequently, exact size groupings may only be applicable to the particular salinity regime (19–25 ppt) that we sampled. However, samples were taken throughout peak spawning for black drum and silver perch and may encompass the ranges that occur for these species in lower Chesapeake Bay.

Results of our genetic analysis suggest that identifications of eggs of spring-spawning Sciaenidae in

Table 2

Common fragment sizes produced by restriction endonuclease (*Hin*dIII) digestion of mtDNA purified from ovarian tissue of spring spawning sciaenids.

Species	Fragment sizes (Kb)						
Bairdiella chrysoura	5.0	3.9	2.8	1.9	1.7	1.7	1.3
Cynoscion nebulosus	8.5	4.5	3.8[1]				
Cynoscion regalis	5.6	4.3	4.1	2.9			
Menticirrhus saxatilis	5.4	3.2	2.4	2.0	1.9	1.8	
Pogonias cromis	3.3	2.9	2.7	2.5	2.1	1.3	1.0

[1] J. Gold, Texas A&M, College Station, TX, pers. commun. 1993.

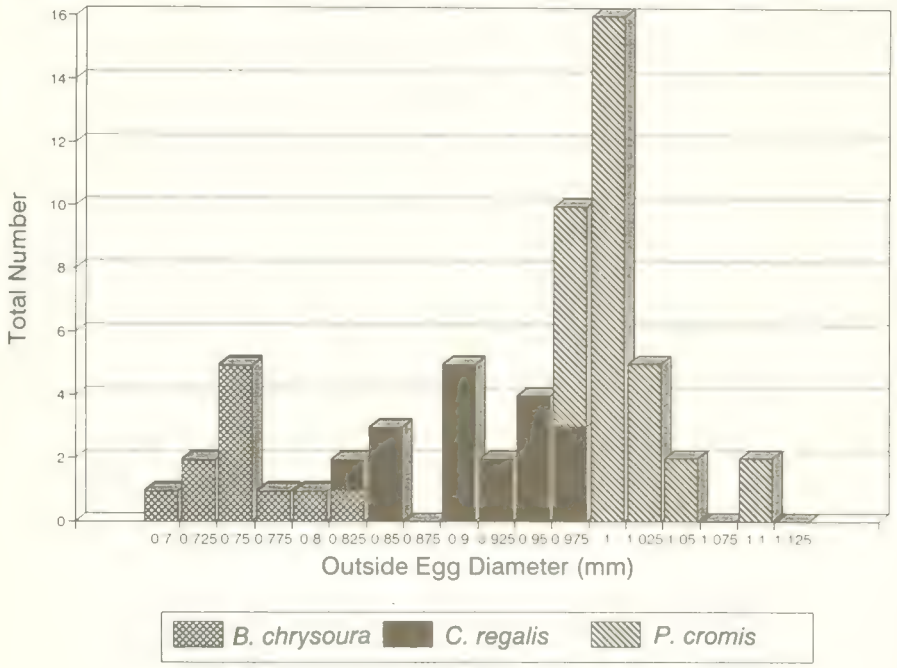

Figure 3

Size distributions of all eggs morphologically typed as sciaenids and identified using genetic techniques.

lower Chesapeake Bay based on OED are subject to error. These findings are particularly timely in light of the increased use of fishery-independent assessments of stock size that require precise estimates of egg abundance (egg production method). Because eggs of black drum and weakfish are spatio-temporally coincident and OEDs overlap, estimates of egg production by black drum in lower Chesapeake Bay may be over-estimated by 50% or greater if identification criteria are based solely on egg size. Likewise, measures of spawning stock biomass will be similarly over-estimated, results that could significantly impact management decisions. Comparable biases in estimates of egg production and spawning stock biomass of weakfish could result from egg misidentifications. However, the more protracted spawning season and greater area of spawning for weakfish in Chesapeake Bay (Olney, 1983) would make these impacts much less severe.

Biochemical techniques are an important tool for the further study of eggs of sciaenids. Genetic analysis has the potential to produce reliable results and permit the storage of samples for later analysis. Additional studies are needed to survey genetic identifications over the entire spawning season and area to determine if egg sizes change over time or are influenced by seasonal changes in hydrography or by age structure of the spawning stock. Finally, the use of genetic techniques, coupled with an extensive examination of morphology could lead to the delineation of other characters that may be useful in separating the eggs of these species.

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Literature cited

Brown, N. J.
1981. Reproductive biology and recreational fishery for spotted seatrout, *Cynoscion nebulosus*, in the Chesapeake Bay area. M.A. thesis, College of William and Mary, Williamsburg, 119 p.

Comyns, B. H., J. Lyczkowski-Shultz, D. L. Nieland, and C. A. Wilson.
1991. Reproduction of red drum, *Sciaenops ocellatus*, in the northcentral Gulf of Mexico: seasonality and spawner biomass. *In* R. D. Hoyt (ed.), Larval fish recruitment and research in the Americas: proceedings of the thirteenth annual larval fish conference, p. 17–26. Dep. Commer., NOAA Tech. Rep. NMFS 95.

Cowan, J. H., R. S. Birdsong, E. D. Houde, J. S Priest, W. C. Sharp, G. B. Mateja.
1992. Enclosure experiments on survival and growth of black drum eggs and larvae in lower Chesapeake Bay. Estuaries 15(3):392–402.

deSylva, D. P., F. A. Kalber Jr., and C. N. Shuster.
1962. Fishes and ecological conditions in the shore zone of the Delaware River estuary, with notes on other species collected in deeper water. Univ. Del. Mar. Lab. Inf. Ser. Publ. 51, 164 p.

Ditty, J. G.
1989. Separating early larvae of sciaenids from the western North Atlantic: a review and comparison of larvae off Louisiana and Atlantic coast of the U.S. Bull. Mar. Sci. 44(3):1083–1105.

Fable, W. A., Jr., T. D. Williams, and C. R. Arnold.
1978. Description of reared eggs and young larvae of the spotted seatrout *Cynoscion nebulosus*. Fish. Bull. 76 (1):65–72.

Gold, J. R., L. R. Richardson, C. Furman, and T. L. King.
1993. Mitochondrial DNA differentiation and population structure in red drum (*Sciaenops ocellatus*) from the Gulf of Mexico and Atlantic Ocean. Mar. Biol. 116(2):175–185.

Graves, J. E., M. A. Simovich, and K. M. Schaefer.
1988. Electrophoretic identification of early juvenile yellowfin tuna, *Thunnus albacares*. Fish. Bull. 86(4):835–838.

Graves, J. E., M. J. Curtis, P. A. Oeth, and R. S. Waples.
1990. Biochemical genetics of southern California basses of the genus *Paralabrax*: specific identification of fresh and ethanol-preserved eggs and early larvae. Fish. Bull. 88:59– 66.

Graves, J. E., J. R. McDowell, and M. L. Jones.
1992. A genetic analysis of weakfish, *Cynoscion regalis*, stock structure along the mid-Atlantic coast. Fish. Bull. 90:469–475.

Holt, G. J., S. A. Holt, and C. R. Arnold.
1985. Diel periodicity of spawning in sciaenids Mar. Ecol. Prog. Ser. 27:1–7.

Holt, S. A., G. J Holt, and L. Young-Abel.
1988. A procedure for identifying sciaenid eggs. Contr. Mar. Sci. 30:99–108.

Johnson, G. D.
1978. Development of fishes of the mid-Atlantic bight. Vol. IV: Carangidae through Ephippidae. Fish Wildl. Serv., U.S. Dep. Interior, 314 p.

Joseph, E. B., W. H. Massman, and J. J. Norcross.
1964. The pelagic eggs and early larval stages of the black drum from Chesapeake Bay. Copeia 1964:425–434.

Lansman, R. A., J. C. Avise, C. F. Aquadro, J. F. Shapira, and S. W. Daniel.
1981. The use of restriction endonucleases to measure mtDNA sequence relatedness in natural populations. III: techniques and potential applications. J. Mol. Evol. 17:214–226.

Lippson, A. J., and R. L. Moran.
1974. Manual for identification of early developmental stages of fishes of the Potomac River estuary. Maryland Dep. Natl. Resources, Power Plant Sitting Prog. Rep. PPSP-MP-13, 282 p.

Merriman, D. and R. C. Sclar.
1952. The pelagic fish eggs and larvae of Block Island Sound. Bull. Bingham. Oceanogr. Collect. Yale Univ. 13(3):156–219.

Morgan, R. P.
1975. Distinguishing larval white perch and striped bass by electrophoresis. Chesapeake Sci. 16:68–70.

Olney, J. E.
1983. Eggs and early larvae of the bay anchovy, *Anchoa mitchilli*, and the weakfish, *Cynoscion regalis*, in lower Chesapeake Bay with notes on associated ichthyoplankton. Estuaries 6(1):20–35.

Olney, J. E., and E. D. Houde.
1993. Evaluation and use of *in situ* silhouette photography in studies of estuarine zooplankton. Bull. Mar. Sci. 52(2):845–872.

Olson, R. R., J. A. Runstadler, and T. D. Kocher.
1991. Whose larvae? Nature 351:357–358.

Pearson, J. G.
1929. Natural history and conservation of the red drum and other commercial sciaenids on the Texas coast. U.S. Bur. Fish. Bull. 44:129–214.

Sambrook, J., E. F. Fritsch, and T. Maniatis.
1989. Molecular cloning: a laboratory manual, 2nd ed. Cold Spring Harbor Laboratory Press, NY.

Saucier, M. H., and D. M. Baltz.
1992. Spawning site selection by spotted seatrout, *Cynoscion nebulosus*, and black drum, *Pogonias cromis*, in Louisiana. Environ. Biol. Fishes 36:257–272.

Saucier, M. H., D. M. Baltz, and W. A. Roumillat.
1992. Hydrophone identification of spawning sites of spotted seatrout, *Cynoscion nebulosus* (Osteichthys: Sciaenidae) near Charleston, South Carolina. N.E. Gulf Sci. 12(2):141–145.

Silberman, J. D., and P. J. Walsh.
1992. Species identification of spiny lobster phyllosome larvae via ribosomal DNA analysis. Mol. Mar. Biol. Biotech. 1(3):195–205.

Smith, P. J., and P. G. Benson.
1980. Electrophoretic identification of larval and 0–group flounders (*Rhombosolea* spp.) from Wellington Harbor, N.Z. J. Mar. Freshwater Res. 14:401–404.

Welsh, W. W., and C. M. Breeder Jr.
1923. Contribution to life histories of Sciaenidae of the eastern United States coast. U.S. Bur. Fish. Bull. 39:141–201.

Wisner, B. W.
1965. McClane's standard fishing encyclopedia. Holt, Rhinehart and Winston, Inc., New York, NY, 1057 p.

Abstract.—The Atlantic spadefish *(Chaetodipterus faber)* is the only member of the family Ephippidae in the western Atlantic Ocean and its life history is poorly understood. We redescribe Atlantic spadefish larvae, discuss their relationship to known larvae of other ephippid genera, and discuss the distribution, abundance, and seasonal occurrence of Atlantic spadefish in the northern Gulf of Mexico. Larval Atlantic spadefish are characterized by a small, peak-like, median supraoccipital crest with a single, dorsally directed spine; large preopercle spines, numerous serrate ridges, and other spines on the head; a deep, robust body which becomes laterally compressed; heavy body pigmentation; and early development of specialized spinous scales or "prescales" (at about 5.5-mm standard length [SL]). Transition to juvenile stage begins about 8.0–8.5 mm SL. Developmental morphology and head spination of Atlantic spadefish is similar to that of Pacific spadefish, *Chaetodipterus zonatus*. Sequence of fin completion is pelvics — dorsal and anal soft rays — dorsal spines–pectorals. Overall, ≥85% of Atlantic spadefish larvae were found in waters ≥28.0°C and between 26.7 and 31.3 ppt. Larvae occur primarily in coastal waters, except near the Mississippi River delta, an area with a narrow shelf and rapidly increasing water depths. Delta waters may offer additional habitat suitable to Atlantic spadefish larvae because of lower salinities. Larvae are primarily collected between June and August and in the north-central Gulf of Mexico. Larval Atlantic spadefish are apparently rare in the eastern Gulf off Florida. Catch rates near the Mississippi River delta during August were higher than elsewhere in the north-central Gulf and suggest a possible association with riverine frontal areas which requires further study.

A re-description of Atlantic spadefish larvae, *Chaetodipterus faber* (family: Ephippidae), and their distribution, abundance, and seasonal occurrence in the northern Gulf of Mexico

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The percoid family Ephippidae is usually considered to comprise five genera and 17 species (Nelson, 1984). The Atlantic spadefish *(Chaetodipterus faber)* is the only member of this family in the western Atlantic Ocean. Rare north of Chesapeake Bay, Atlantic spadefish inhabit coastal waters which extend southward to Brazil (Johnson, 1978). Historically, Atlantic spadefish represented a relatively minor portion of recreational fisheries. Nevertheless, fishing tournaments are currently being used to stimulate interest in their fisheries (Schmied and Burgess, 1987). Ryder (1887) described eggs and yolk-sac larvae of Atlantic spadefish, but Johnson (1978) questioned the identity of these specimens. Larvae ≥2.5 mm standard length (SL) are described and illustrated by Hildebrand and Cable (1938), but this study is insufficient to examine important developmental details and is based on the static rather than dynamic approach to larval description (Berry and Richards, 1973). Finucane et al.[1] illustrated 5.1- and 6.4-mm SL Atlantic spadefish. Johnson (1984) commented on cranial morphology and provided insight on the value of larval characters in resolving the relations among ephippids and their relation to other families. Aspects of juvenile and adult life history are discussed for Atlantic spadefish from South Carolina waters (Hayse, 1990), but the distribution, abundance, and seasonal occurrence of Atlantic spadefish larvae are poorly understood. Our objectives are to redescribe the development of Atlantic spadefish larvae, discuss their relation to known larvae of other ephippid genera, and to describe the distribution, abundance, and seasonal occurrence of Atlantic spadefish larvae in the northern Gulf of Mexico (Gulf).

Materials and methods

The distribution, abundance, and seasonal occurrence of larval Atlan-

[1] Finucane, J. H., L. A. Collins, L. E. Barger, and J. D. McEachran. 1979. Ichthyoplankton/mackerel eggs and larvae. Environmental studies of the south Texas outer continental shelf, 1977. Final Rep. to Bur. Land Manage., Wash., DC, Southeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Galveston, TX 77550, 504 p.

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[2] Contribution No. LSU-CFI-92-7 of Louisiana State University Coastal Fisheries Institute.

tic spadefish were determined from collections taken primarily during Southeast Area Monitoring and Assessment Program (SEAMAP) ichthyoplankton surveys of the Gulf between 1982 and 1986 (SEAMAP[2]). These years represent the first time interval for which a complete set of data were currently available. Latitude 24°30' N was the southern boundary of our study area in the eastern Gulf, a cutoff which approximates the continental shelf break off the southern tip of Florida. Latitude 26°00' N was the southern boundary of the central and western Gulf. These coordinates approximate the U.S. Exclusive Economic Zone (EEZ)/Fishery Conservation Zone (FCZ).

Standard ichthyoplankton survey techniques as outlined by Smith and Richardson (1977) were employed in data collection. Stations sampled by National Marine Fisheries Service (NMFS) vessels were arranged in a systematic grid of about 55–km intervals. NMFS vessels primarily sampled waters >10 m deep. Each cooperating state had its own sampling grid and primarily sampled their coastal waters. Hauls were continuous and made with a 60–cm bongo net (0.333–mm mesh) towed obliquely from within 5 m of the bottom or from a maximum depth of 200 m. A flowmeter was mounted in the mouth of each net to estimate volume of water filtered. Ship speed was about 0.75 m/sec; net retrieval was 20 m/min. At stations <95 m deep, tow retrieval was modified to extend a minimum of 10 minutes in clear water or 5 minutes in turbid water. Tows were made during both day and night depending on when the ship occupied the station. Overall, 1,823 bongo net tows were made between 1982 and 1986. The SEAMAP effort between 1982 and 1984 also involved the collection and processing of 814 neuston samples taken with an unmetered 1×2 m net (0.947–mm mesh) towed at the surface for 10 minutes at each station. SEAMAP sampling during April and May was conducted primarily off the continental shelf; sampling during March, and from June through December, was conducted primarily over the shelf at stations <180 m deep. Additional information on the spatial and temporal coverage of SEAMAP plankton surveys is found in Stuntz et al. (1985), Thompson and Bane (1986, a and b), Thompson et al. (1988), and Sanders et al. (1990). Atlantic spadefish larvae were also obtained from surface-towed 1×2 m neuston net collections (0.947–mm mesh, 71 samples) made by the National Marine Fisheries Service (NMFS, Panama City, Florida) during August 1988. These NMFS collections were associated with riverine/oceanic frontal zones off the Mississippi River delta. Frontal zones near the delta were not sampled during either June or July.

A detailed examination of Atlantic spadefish larvae was made to describe developmental morphology. Body measurements were made on 21 Atlantic spadefish larvae between 1.9 and 12.5 mm (Table 1) and follow Hubbs and Lagler (1958) and Richardson and Laroche (1979). Measurements were made to the nearest 0.1 mm with an ocular micrometer in a dissecting microscope. We follow Leis and Trnski's (1989) criteria for defining length of preopercular spines, body depth, head length, eye diameter, and the eye diameter/head length ratio. We consider notochord length in preflexion and flexion larvae synonymous with SL in postflexion larvae and report all lengths as SL unless otherwise noted. Specimens were field-fixed in 10% formalin and later transferred to 70% ethyl alcohol. Terminology for

[2] SEAMAP. 1983–1987. (plankton). ASCII characters. Data for 1982–1986. Fisheries-independent survey data/National Marine Fisheries Service, Southeast Fisheries Center: Gulf States Marine Fisheries Commission, Ocean Springs, MS (producer).

Table 1

Morphometrics of larval Atlantic spadefish (*Chaetodipterus faber*) from the northern Gulf of Mexico. Measurements are expressed as % standard length (SL) and rounded to the nearest whole number

SL	*N*	Preanal length	Head length	Snout length	Orbit diameter	Body depth pectoral	Prepelvic distance
1.8–2.9	3	42–55	21–31	3–8	13–15	34–44	—
3.0–4.9	3	54–65	35–43	5–7	15–17	50–60	30–36
5.0–6.9	4	60–61	30–42	5–6	15–18	56–63	30–35
7.0–8.9	4	61–64	35–39	7–9	14	55–64	27–37
9.0–10.9	4	59–61	34–35	6–8	13–14	60–65	27–34
11.0–11.9	2	54–56	34–35	7–9	14	60–65	27
12.5	1	60	36	8	14	68	36

location of head spines followed Gregory (1933). One larva was cleared with trypsin then stained with alizarin in each millimeter (mm) length interval to examine small serrate ridges around the orbit (i.e. circumorbital bones), and spines and ridges on the head. We examined spines on the occipital and frontal bones with a scanning electron microscope (SEM), and specialized spinous scales with a compound microscope. Fin rays were counted when first segmented and spines when present. Representative specimens were illustrated with the aid of a camera lucida.

Estimates of larval density (number of larvae/$100m^3$ of water) and catch (number of larvae/10 tow) were calculated by month. Months were combined across years because not all months were sampled every year (Appendix Table). Densities for stations where larvae were collected (i.e. positive catch stations) were calculated by dividing sum of larvae collected in bongo net tows by total positive catch station volume of water filtered (VWF) and multiplying the result by 100. In addition, an overall (i.e. grand) density estimate was calculated by dividing sum of larvae by total VWF for all stations sampled that month and multiplying the result by 100. Overall density more closely reflects the density of larvae throughout the area by including the total volume of water filtered in calculations. Estimates of larval catch in neuston nets were calculated by dividing sum of larvae by number of positive catch neuston stations or by total number of neuston stations sampled and multiplying the result by 10. Estimates of larval density and catch included stations at long. ≥88°00' W because only one Atlantic spadefish larva was collected east of Mobile Bay, Alabama. Similarly, estimates were calculated only for June through August because May and September had but one positive catch station each.

Temperature and salinity data were gathered from the sea surface. Positive catch station hydrographic data were multiplied by total number of larvae collected at each station to obtain a monthly median and mean. Hydrographic data were also combined across months to obtain an overall (i.e. grand) median and mean. This method gives weight to distribution of larvae rather than to distribution of stations. We used a percent cumulative frequency of ≥85% for defining the relation between distribution of Atlantic spadefish larvae and water temperature, salinity, and station depth. Percent frequency indicates the range of hydrographic conditions most often associated with occurrences of larvae. Proc Univariate was used to calculate median, mean, and percent cumulative frequency statistics (SAS Institute, 1985).

Results

Morphometrics and pigmentation

Early larvae were rotund and deep-bodied; body depth was >50% SL by 3.5 mm and ≥60% by 9 mm (Table 1). Atlantic spadefish became increasingly deep-bodied and laterally compressed after notochord flexion. There were 24 myomeres but these became obscured by pigment in postflexion larvae. The head was large and averaged about 35% SL in larvae >3.0 mm. Head profile became steep and increasingly deeper than long. The mouth was terminal and the upper jaw reached to about mid-eye. Eyes were round and large, ranging from 36 to 43% of head length in larvae >3.5 mm (i.e. about 14–15% SL). The gut was tightly coiled in a single loop and the anus was slightly beyond mid-body (usually 55–60% SL).

Pigment was largely restricted to the anterior-half of the body in early preflexion larvae of Atlantic spadefish. On the head of a 1.8-mm larva, external pigment was scattered over the mid- and hindbrain, nape, opercle, branchiostegal membrane, and along the isthmus and quadrate. Internally, pigment was present along and above the anterior portion of the notochord, and a single median patch was observed on the roof of the mouth. On the abdomen, there was a patch of pigment on the visceral mass immediately anterior to and below the pectoral-fin base. In addition, melanophores were scattered over the pectoral fin base and its finfold and were distributed laterally over the visceral mass and hindgut. A row of about 20–25 small, closely spaced melanophores were visible along the ventral midline of the tail in early larvae. Number of melanophores along the ventral midline of the tail decreased as larvae grew. Melanophores on the nape, opercle, pectoral-fin base, and visceral mass formed a "swath" of pigment over the anterior 55–60% of the body by 2.5–3.0 mm (Fig. 1). By 3.0–3.5 mm, internal melanophores were visible anteriorly on the forebrain and laterally on the midbrain above the eye. Melanophores were also scattered both internally and externally over the hindbrain both anterior to and posterior to the base of the supraoccipital crest. By early postflexion (i.e. 5.0 mm), the head and abdomen were densely pigmented but the posterior portion of the body was sparsely pigmented. Pigmentation increased on the posterior-half of the body as larvae grew, and by 10.0 mm the entire body was pigmented (Fig. 1). Consolidation of pigment into bands began on the head of Atlantic spadefish larvae with one band visible above the eye by 10.0–11.0 mm. This band of pigment was enclosed by indefinite, pale crossbars. The

anterior pale crossbar was situated above the middle of the eye and the posterior crossbar was behind the eye, extending mid-way down the preopercle. Larvae <12.5 mm had only one band of pigment (Fig. 1).

The pelvics were the first fins to have pigment. Pelvic fin buds were pigmented by 4.0 mm; the pelvics were densely pigmented thereafter. Pigment appeared on the pectoral fin along the proximal portion of the rays at about 4.0–4.5 mm. Melanophores were lightly scattered over the pectoral fin in the largest specimen examined (Fig. 1). Melanophores were scattered over the membrane covering the anterior-most dorsal spines by about 6.0 mm and the anal spines by about 8.0 mm. Melanophores were added along the dorsal and anal fins as larvae developed, covering the proximal-third of each soft ray in the largest specimen examined. Pigment was present along the proximal portion of the central rays of the caudal fin by 11.0 mm (Fig. 1).

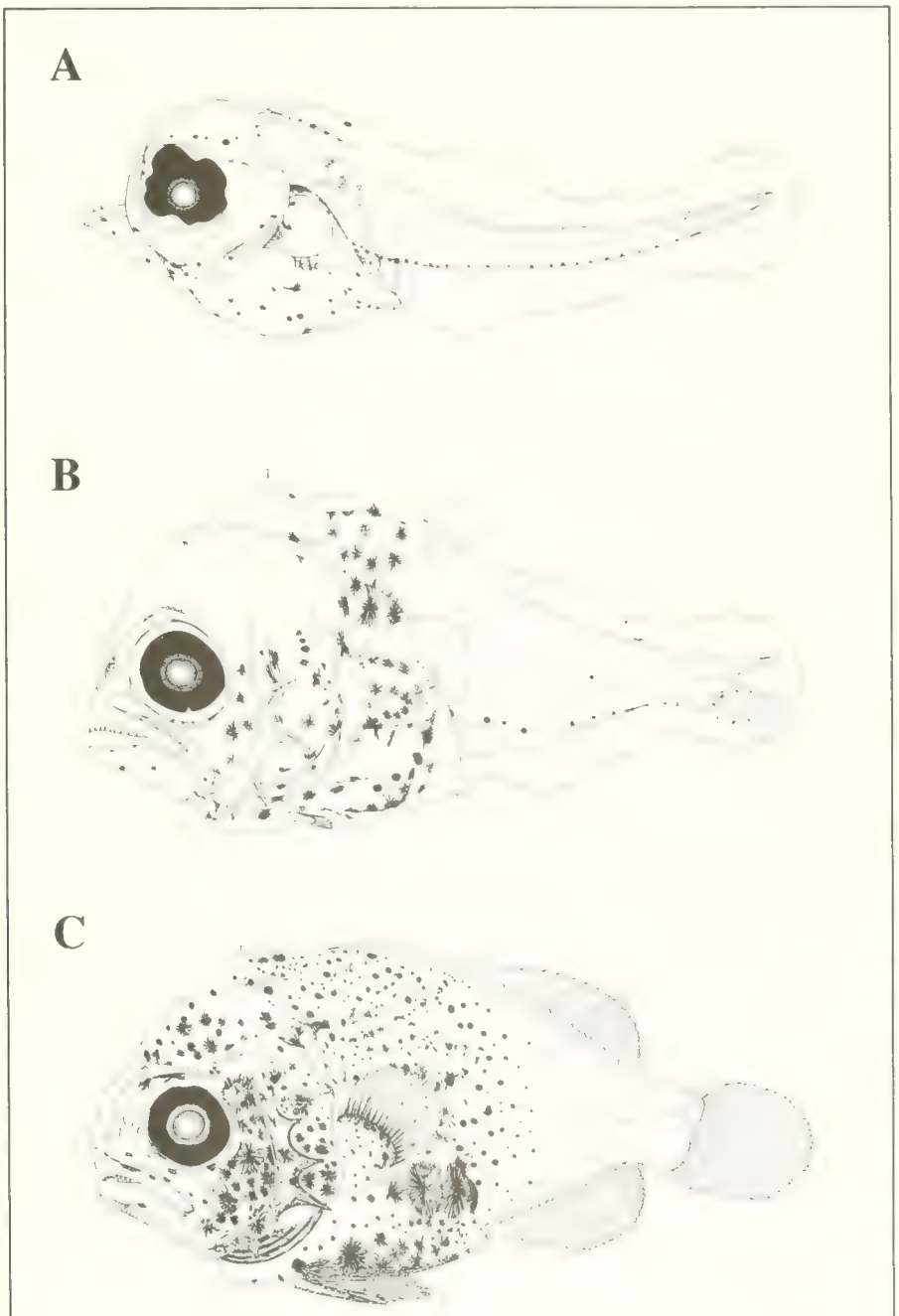

Figure 1

Larval development of Atlantic spadefish, *Chaetodipterus faber*, from the northern Gulf of Mexico. (**A**)1.8 mm; (**B**) 3.5 mm; (**C**) 5.0 mm; (**D**) 7.0 mm; (**E**) 11.6 mm. All measurements are standard length (SL).

Head and body spination

Atlantic spadefish larvae develop two series of preopercular spines, one along the posterior margin of the outer shelf and the other along the inner shelf. Both the outer and inner shelf have dorsal and ventral limbs. Three preopercular spines were present along the outer shelf of a 1.8-mm larva, the largest of which was present at its preopercular angle (Fig. 1). A fourth and a fifth spine were added by 3.5 mm, one dorsal and one ventral to the angle of the preopercle. A sixth preopercular spine, smaller than the others and often difficult to locate, was present by 5.0 mm. This sixth spine was the anterior-most spine along the ventral limb of the exterior shelf and was resorbed by 11.0–12.0 mm in some specimens. One larva we examined had seven preopercular spines along the outer shelf but most had two spines along the dorsal limb, one at the angle, and three along the ventral limb (Fig. 2). Spines along the outer shelf were simple. Two to three spines were also present along the inner shelf of the preopercle by 3.5 mm. Number of spines along the inner shelf increased as larvae grew, resulting in a serrate margin (Fig. 2). A small, poorly developed opercle

spine was forming by 5.0 mm and was difficult to locate on larvae not cleared and stained. A spine also was present along the posterior margin of the interopercle near its junction with the subopercle by 6.0 mm (Fig. 2). The interopercular spine often was hidden by the large spine at the preopercular angle but was more easily located as the preopercular angle spine regressed.

Atlantic spadefish larvae have numerous spines and ridges scattered over the head. A thickened ridge was visible dorsally along the supraoccipital of 2.0-mm larvae. This thickened ridge became a small, peak-like, median supraoccipital crest with a single, dorsally directed spine by 2.5 mm. The supraoccipital spine began to regress by 5.0 mm and was resorbed by 10.0–10.5 mm. A supraorbital ridge was present by 3.5 mm. This ridge became serrate by 4.0 mm. Small serrate ridges were visible along the dorsal margin of both the lacrimal and jugal bones (i.e. first and second suborbitals; Gregory, 1933) and third suborbital bone by 5.0 mm. Spines or spinous ridges were also visible along the fourth and fifth suborbitals, dermosphenotic (i.e. sixth suborbital), posttemporal, pterotic, tabular, and supracleithral bones by 6.0 mm. The ventral margin of the jugal bone near the posterior margin of the maxillary had a single, ventrally directed spine by 7.0 mm (Fig. 2). Individual spines were also scattered over the frontal and occipital bones of young Atlantic spadefish. The bases of these spines were covered by integument so that only a portion of each spine was visible (Fig. 3). All head spines and spinous ridges were present in the largest specimen examined (12.5 mm) but were difficult to locate on larvae not cleared and stained because of heavy body pigment.

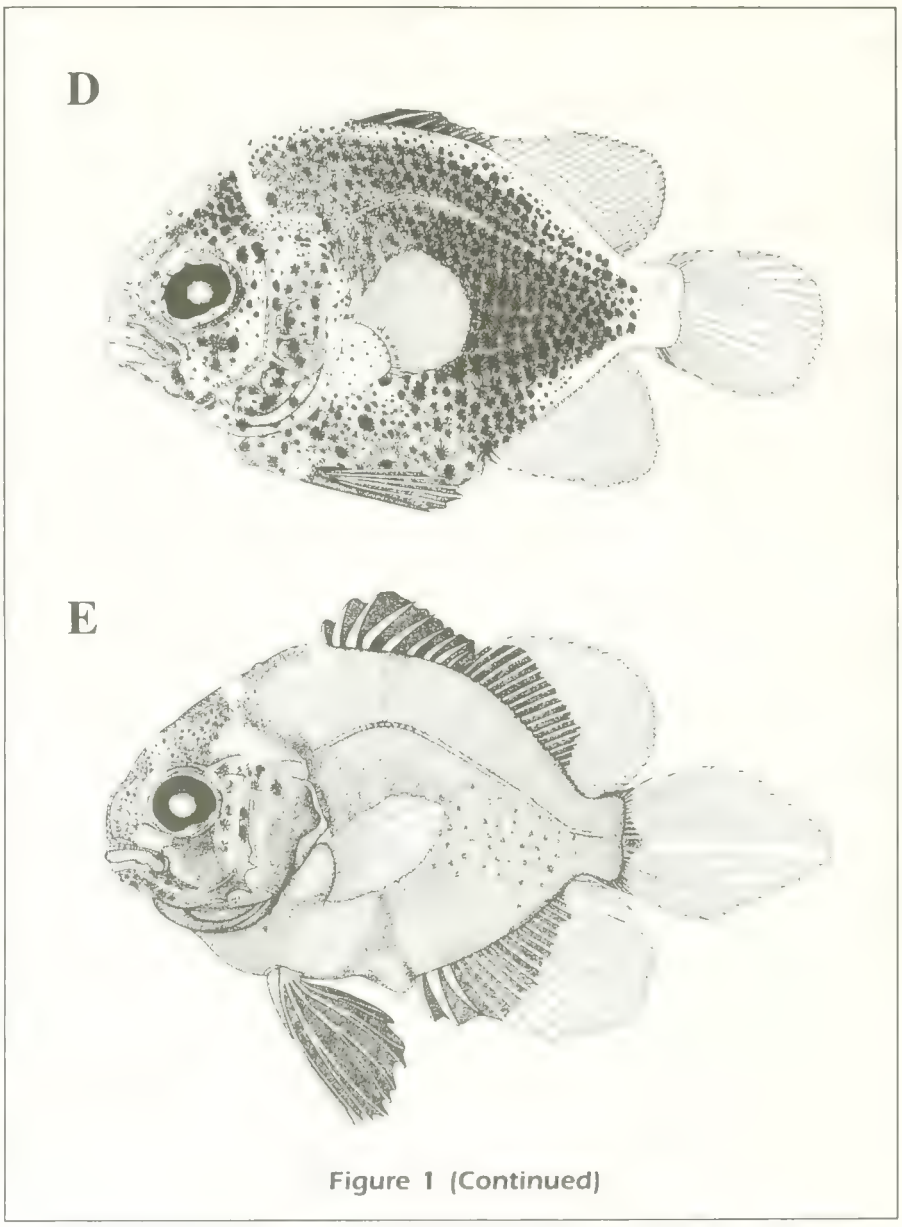

Figure 1 (Continued)

Teeth in Atlantic spadefish were placed in an inner and outer band. Teeth first appeared in a single band on the premaxillary and anteriorly on the dentary at about 2.5 mm. Teeth were pointed and closely spaced. A second band of teeth formed along the upper and lower jaws by 4.0 mm; the outer band was slightly larger than the inner band. Teeth were added along the upper and lower jaws as larvae developed (Figs. 1 and 2).

Specialized spinous scales or "pre-scales" began to develop at about 5.5 mm. Pre-scales were characterized by a single, elevated, posteriorly directed spine that was positioned near the center of the scale. Pre-scales developed first on the head and later appeared anteriorly along the lateral midline. Pre-scales were added outward toward the dorsal and ventral midlines and proceeded in a posterior direction, covering the body by 10.0 mm.

The first bones to ossify were the preopercular spines, supraoccipital crest, premaxillary, dentary, and cleithrum. Three predorsal bones (i.e. supra-

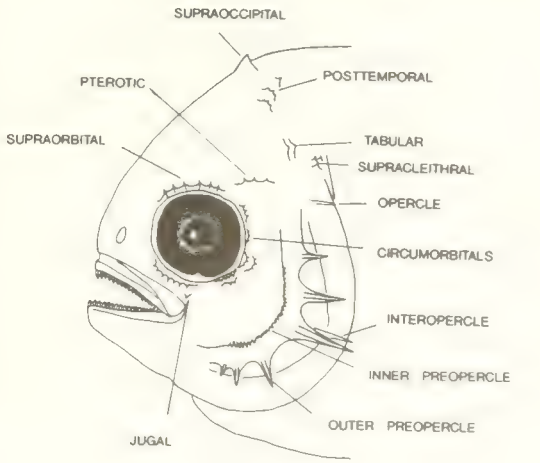

Figure 2

Location of head spines on a 7.0-mm SL larva of Atlantic spadefish, *Chaetodipterus faber*, from the northern Gulf of Mexico.

neurals) were ossifying by 6.0 mm. The anteriormost precaudal vertebrae and dorsal- and anal-fin pterygiophores ossified first; ossification proceeded posteriorly. All caudal bones were ossifying by 8.0 mm. Six branchiostegal rays and 10+14 vertebrae were present in all cleared and stained specimens.

Fin development

A continuous median finfold extended around the body from the nape to the anus of early larvae. Fin ray anlagen began forming obliquely downward in the caudal finfold during flexion (usually 3.5–4.5 mm). Caudal-fin ray development proceeded outward from mid-base as the hypural complex shifted to a terminal position, with the adult complement of 9+8 principal rays attained at about 6.0 mm (Table 2). Development of the dorsal- and anal-fin bases coincided with notochord flexion. Both fin bases and their ray anlagen began to differentiate near mid-fin; development proceeded outward from mid-fin. All dorsal and anal soft rays were present by about 7.0 mm. Soft dorsal and anal fin ray complements were present before their spines (Table 2); dorsal and anal spines developed in an anterior

Figure 3

Scanning electromicrograph of the frontal and occipital spines of a 7.0-mm SL Atlantic spadefish, *Chaetodipterus faber*. Epithelium was partially digested with trypsin to enhance visibility of frontal and occipital spines. Magnification: 140×.

to posterior direction. Pelvic fins were precocious and heavily pigmented. Pelvic buds were visible by 4.0 mm; pelvics had a full complement of elements (I, 5) by 6.0 mm. Pectoral rays began to develop by 5.0 mm and a full complement (17) was present by 8.0 mm. Sequence of fin completion was pelvics – soft dorsal and anal rays – dorsal spines – pectorals. A full complement of elements in all fins by 8.0–8.5 mm marked the beginning of transition to the juvenile stage (Table 2).

Table 2

Fin-ray counts of larval Atlantic spadefish *(Chaetodipterus faber)* from the northern Gulf of Mexico.

Length (mm SL)[1]	Dorsal	Anal	Pectoral	Pelvic	Caudal
4.3	III, Anlagen	8	Anlagen	Anlagen	0–7+7–0
5.0	III, 14	11	7	4	0–6+6–0
6.1	VII, 24	II, 17	13	I, 5	3–9+8–3
7.0	VII, 23	II, 18	16	I, 5	4–9+8–5
8.3	IX, 21	III, 17	17	I, 5	4–9+8–4
9.3	IX, 21	III, 18	17	I, 5	5–9+8–4
10.0	VIII, 23	III, 18	17	I, 5	5–9+8–5

[1] One larva of each length.

Temporal and spatial distribution

Alantic spadefish larvae were collected from May through September primarily in the north-central Gulf. Larvae were usually collected between June and August, density being highest during June and catch highest during August (Table 3). Larval Atlantic spadefish were especially abundant near the Mississippi River delta during August 1988, when 19 of 72 neuston tows (26%) associated with riverine frontal zones collected larvae. During August 1984, however, <5% of neuston tows (n=162) from other areas of the north-central and western Gulf not associated with the delta captured larvae. Only one Atlantic spadefish larva was collected east of Mobile Bay, Alabama (long. 88°00' W). This 4.0-mm specimen was found off Apalachicola Bay (Florida) during August 1984 at a station 13 m deep (Fig. 4). Salinity at this station (34.2 ppt) was the highest recorded with a positive catch during the study. The largest specimen collected in surface-towed nets was 12.5 mm; this observation may indicate that larvae move out of surface waters by this size.

Table 3

Density (number of larvae/100 m^3) and catch (number of larvae/10 neuston tows) of Atlantic spadefish larvae (*Chaetodipterus faber*) from the northern Gulf of Mexico. Months are combined across years (1982–1986, and August 1988). Not all months were sampled each year. Numbers in parentheses are positive catch stations over total stations sampled by month. Monthly density estimates were calculated by dividing sum of larvae by either sum of volume water filtered (VWF) overall, or sum of positive station VWF. Monthly catch estimates were calculated by dividing sum of larvae by number of stations sampled overall or by number of positive catch stations.

Gear	June	July	August
Bongo			
Overall density	0.3[1]	<0.1[2,3]	<0.1[4,5]
Positive density	6.2 (19/341)	1.3 (4/134)	1.5 (4/221)
Neuston			
Overall catch	4.0	0.4	17.0
Positive catch	42.6 (19/201)	13.3 (3/92)	131.6 (32/248)

[1] Total VWF – 43,730 m^3, positive catch station VWF – 1,799 m^3, number of larvae collected was 111.
[2] 0.02/100 m^3.
[3] Total VWF – 22,207 m^3, positive catch station VWF – 381 m^3, number of larvae collected was 5.
[4] 0.03/100 m^3.
[5] Total VWF – 35,174 m^3, positive catch station VWF – 796 m^3, number of larvae collected was 12.

Overall, ≥85% of Atlantic spadefish larvae were collected in surface waters ≥28.0°C (median: 28.1°C, mean: 28.7°C, range: 25.0°–32.2°C), at salinities between 26.7 and 31.3 ppt (median: 28.8 ppt, mean: 28.4 ppt, range: 11.8–34.2 ppt), and at station depths <238 m (median: 83 m, mean: 139 m, range: 9–470 m) (Fig. 5). However, distribution of larvae versus station depth was strongly influenced by two very large neuston-net collections of 192 and 64 larvae during August 1985 which represented 40% of all larval Atlantic spadefish taken. These two stations were located in waters near the shelf edge, 50 and 75 km east of the Mississippi River delta (28.1°C, 30.1 ppt, 235 m deep; 27.9°C, 28.1 ppt, 238 m deep, respectively). Other stations had 27 or fewer larvae. Distribution of larvae versus station depth without the two large collections shifted median station depth

shoreward from 83 to 26 m; larvae may, therefore, primarily inhabit coastal waters. This shoreward shift in median station depth was reinforced by distribution of larvae in bongo net tows and by distribution of larvae during June and July (Fig. 4, Table 4). About 86% of all Atlantic spadefish larvae collected in bongo net tows (n=128) were from waters ≤25 m deep. In addition, distribution of larvae during June and July was shoreward of that during August. Similarly, 51% of all stations where larvae were collected (i.e. 41 of 81) were inside 25 m; 64% were inside 50 m. Only 14% of positive catch stations were located beyond the 100 m isobath; most of these stations were near the Mississippi River delta, an area with a narrow shelf and rapidly increasing water depths.

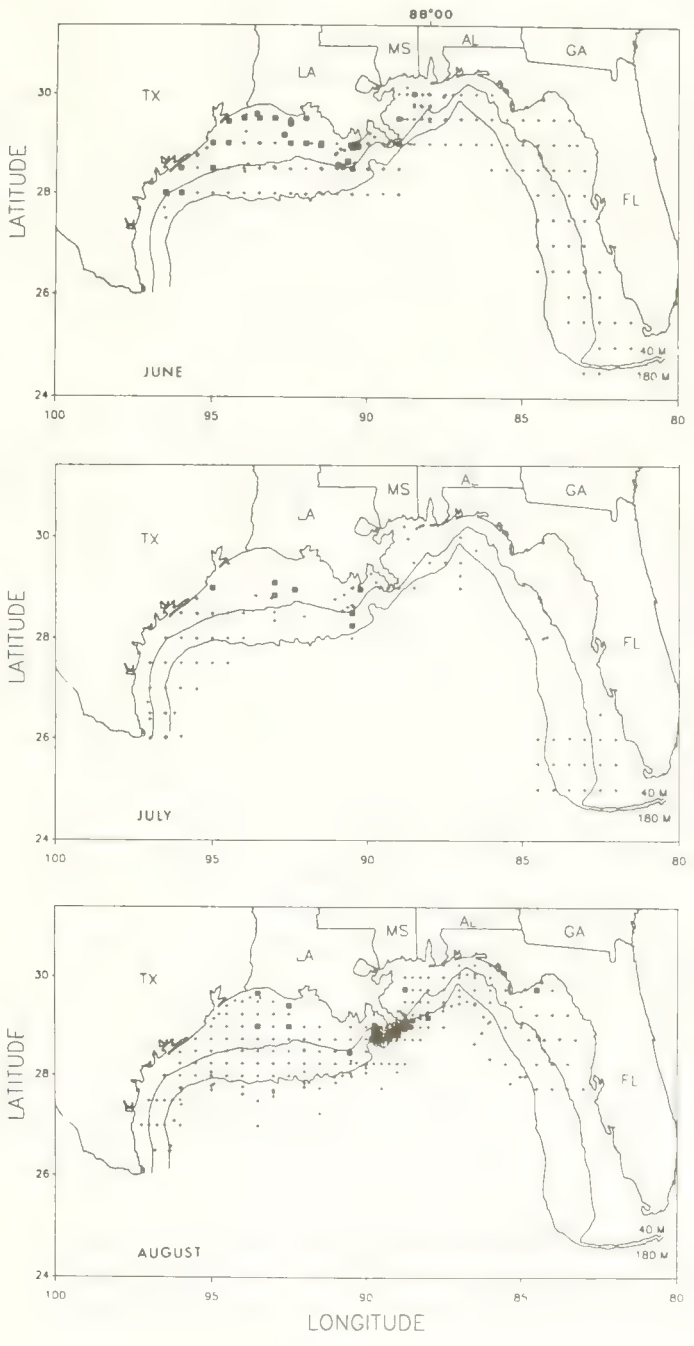

Figure 4

Distribution of Atlantic spadefish larvae (*Chaetodipterus faber*) in the northern Gulf of Mexico by month. Months are combined across years (1982–1986, and August 1988). Not all months sampled each year. Plus (+) signs are total stations sampled and squares are positive catch stations. Distribution of stations are for both bongo and neuston net tows.

Discussion

Our observations on the morphological development of Atlantic spadefish larvae generally agree with Hildebrand and Cable (1938). These authors, however, do not discuss pigment on the roof of the mouth. The presence of a single, median patch of pigment on the roof of the mouth is helpful in identifying early Atlantic spadefish larvae before the supraoccipital crest is clearly visible. Hildebrand and Cable (1938) do not discuss small spines or ridges along the circumorbital bones (i.e. supraorbital, suborbitals, and dermosphenotic) or tabular bone (Fig. 2) but do illustrate serrate ridges above the eye and in the pterotic region (Hildebrand and Cable, 1938, their Figs. 26 and 27). Spination on the circumorbital bones has generally been found only in those larval percoids with cranial ornamentation (Johnson, 1984). Most of these larval percoids also have other specializations, such as spinous scales and an elongate spine at the angle of the preopercle, among other characters (Johnson, 1984). Neither Hildebrand and Cable (1938) nor Johnson (1984) mention the supracleithral spines we found on Atlantic spadefish larvae (Fig. 2) and in larvae of Pacific spadefish, *Chaetodipterus zonatus* (Martinez-Pecero et al., 1990). The "short, hair-like spines on the upper surface of the head" noted by Hildebrand and Cable (1938) on 9.0-mm Atlantic spadefish larvae may be the same spines we found scattered over the frontal and occipital bones (Fig. 3). These frontal and occipital spines are difficult to see under a dissecting microscope because

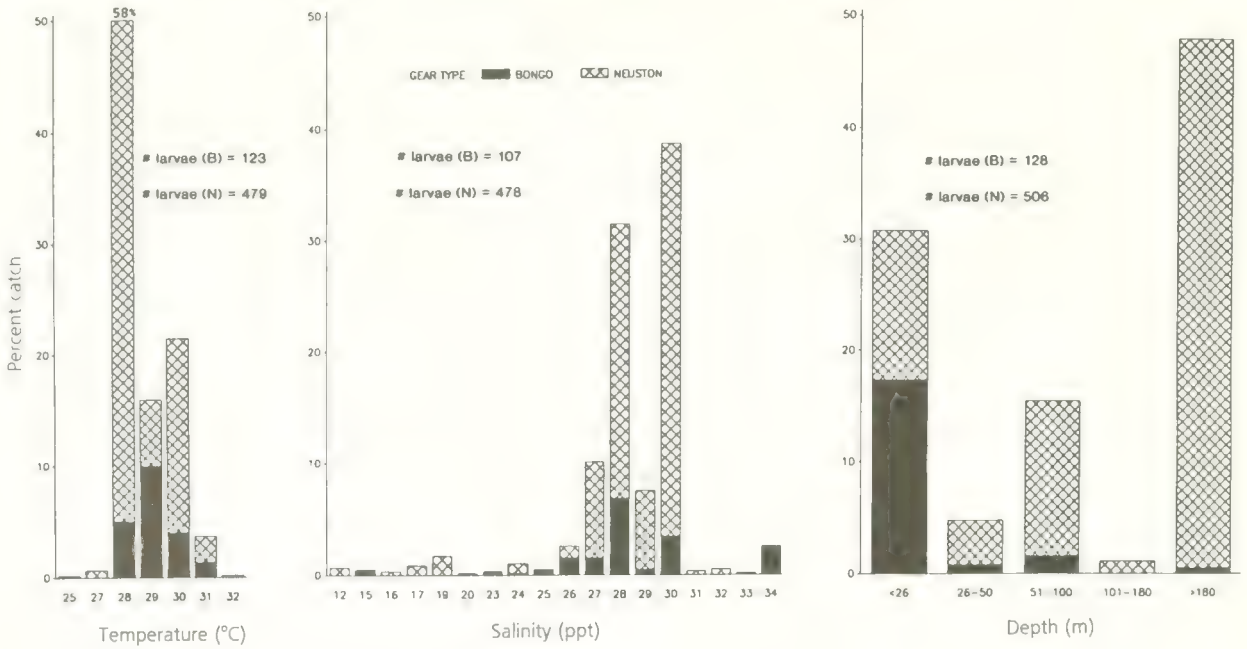

Figure 5

Summary of positive catch station hydrographic data for larval Atlantic spadefish (*Chaetodipterus faber*) from the northern Gulf of Mexico. Percent catch is sum of larvae by interval and gear divided by total number of Atlantic spadefish larvae collected overall. Discrepancies in number of larvae by month among parameters are the result of missing hydrographic data.

Table 4

Summary of hydrographic data by month for Atlantic spadefish (*Chaetodipterus faber*) larvae from the northern Gulf of Mexico. Data are from the surface and for positive catch bongo and neuston net stations only. Station hydrographic data are multiplied by total number of larvae collected at each station to obtain monthly mean and median values.[1] '*N*' is the number of larvae used to obtain mean and median values. Discrepancies in '*N*' by month among parameters resulted from missing hydrographic data.

	Water temperature (°C)				Salinity (ppt)				Station depth (m)			
	N	Mean	Median	Range	*N*	Mean	Median	Range	*N*	Mean	Median	Range
June	160	29.0	29.3	25.0–30.5	143	27.6	27.6	12.1–33.9	192	17.3	16	9–90
July	9	29.4	29.8	29.3–30.5	9	27.6	27.6	25.4–28.6	9	27.3	21	16–70
August	433	28.1	28.6	27.6–32.2	433	28.8	29.4	11.8–34.2	433	194	235	11–470

[1] This method gives weight to distribution of larvae rather than distribution of stations.

they are largely covered by integument. The supraoccipital crest was resorbed by about 10.0–10.5 mm in Gulf larvae but still present on a 11.5-mm specimen from the U. S. Atlantic coast (Hildebrand and Cable, 1938).

The identity of Ryder's (1887) yolk-sac Atlantic spadefish larvae is uncertain (Johnson, 1978). Ryder's 3.5-mm and 4.0-mm larvae lack a supraoccipital crest and preopercular spines, both of which Hildebrand and Cable (1938) and we found by 2.5 mm in Atlantic spadefish larvae. Ryder's 4.0-mm larva also has an oil globule in the yolk sac and the gut does not have the single, tightly coiled loop we found in preflexion Atlantic spadefish. Neither Hildebrand and Cable (1938) nor we found an oil globule in Atlantic spadefish larvae of 2.0 mm or

2.5 mm, respectively. Differences between Ryder's and our study do not support identification of Ryder's larvae <4.0 mm as Atlantic spadefish even if we allow for specimen shrinkage (also noted by Johnson, 1978) and for slower development times due to cooler waters of Chesapeake Bay during the summer when Atlantic spadefish spawn.

Johnson (1984) characterized the sequence of fin completion in larval Atlantic spadefish as pattern A: dorsal and anal soft rays – spinous dorsal – pelvics – pectorals. We cleared and stained seven larvae and found the sequence of fin completion more closely resembles Johnson's (1984) pattern F with all elements of the pelvic fin present before dorsal and anal soft rays. This difference in fin completion pattern, however, may be due to differences in how we and Johnson interpreted spine formation and fin completion. We counted rays when first segmented and spines when present; Johnson may have counted pterygiophores. Pattern F is found in *Hapalogenys*, Monodactylidae, and Pempheridae (Johnson, 1984).

Larvae of Atlantic spadefish are characterized by early development of specialized spinous scales or "prescales" (at about 5.5 mm, this study) that eventually transform into adult ctenoid scales. Spinous larval scales are present to about 15.0 mm (Johnson, 1984). Ctenoid scales are well developed by 18.0 mm (Hildebrand and Cable, 1938).

Developmental morphology and head spination of Atlantic spadefish is generally similar to that of Pacific spadefish (Martinez-Pecero et al., 1990). Both species are deep-bodied (usually 55–60% SL) and preanal length is about 60% SL. Pigmentation and standard length at which fins develop also are similar; a full complement of rays is present in all fins by 8.0–9.0 mm in both species (Hildebrand and Cable, 1938; Martinez-Pecero et al., 1990; this study). However, consolidation of pigment into lateral bands, resorption of the supraoccipital crest, and the beginning of transition to the juvenile stage occur earlier in Pacific spadefish than in Atlantic spadefish. Larvae of ephippids from the Indo-Pacific region differ from *Chaetodipterus* from the western Atlantic and Pacific Oceans in extent of head spination (Leis and Trnski, 1989; Martinez-Pecero et al., 1990; this study). Larvae of *Platax* from the Indo-Pacific have a median supraoccipital crest with a serrate leading edge (Leis and Trnski, 1989) but do not have the circumorbital series of spinous ridges, nor spines on the jugal, tabular, pterotic, or supracleithral bones found in *Chaetodipterus* (Martinez-Pecero et al., 1990; this study). Head spination in *Ephippus* larvae from the Indo-Pacific is similar to that of *Chaetodipterus* and these two genera are probably more closely related than either is to *Platax*. Other species-specific head spination found in *Chaetodipterus* larvae from the western Atlantic and Pacific Oceans, and in *Ephippus orbis*, *Platax batavianus*, and three *Platax* species from the Indo-Pacific region include a posttemporal spine which may be reduced to a ridge in some species, a supraorbital ridge that varies in size among species, and one or two subopercular spines (Leis and Trnski, 1989; Martinez-Pecero et al., 1990; this study).

Early larvae of Atlantic spadefish could be confused with priacanthids, lobotids, some carangids and stromateoids, the wreckfish—*Polyprion americanus,* and *Menticirrhus* spp. because of similarities in head spination or in body pigmentation. Priacanthids have an elongate, serrate, median supraoccipital crest that extends posteriorly over the mid- and hindbrain; serrations along the lower jaw and frontal bone; and the angle preopercular spine is elongate and serrate as is the pelvic spine. Tripletail, *Lobotes surinamensis*, have a vaulted, serrate supraoccipital crest in early larvae, the pelvics are inserted behind the pectoral fins, and have fewer anal fin elements than Atlantic spadefish (Atlantic spadefish: A. III, 17–18, tripletail: A. III, 11–12). In carangids, the two anteriormost anal spines are separated from the third by a distinct gap and most species have a low, median supraoccipital crest that has serrations along the dorsal edge; other carangids lack a supraoccipital crest entirely. Some carangids also have a precocious dorsal fin with anterior spines or rays elongate, or with serrations along the angle preopercular spine. Some stromateoids (e.g. *Ariommus* spp., *Nomeus gronovii*) resemble Atlantic spadefish in early body pigmentation, body shape, and by having precocious pelvics, but stromateoids lack a median supraoccipital crest, a large preopercular angle spine, and all but *Hyperoglyphe* have >30 myomeres. *Polyprion americanus* larvae have a small, peak-like median supraoccipital crest, but with serrations along the leading edge, and lack a serrate pterotic ridge and spines on the tabular bone (Johnson, 1984). Wreckfish also have 27 myomeres, fewer dorsal (22–24) and anal fin (11–13) elements, and the mouth is larger than in Atlantic spadefish. Larval Atlantic spadefish differ from early larvae of *Menticirrhus* spp. by lack of both preopercular spines and the median supraoccipital crest in the latter.

We recently examined specimens reported by Dawson (1971) as larval black driftfish, *Hyperoglyphe bythites*. These specimens had a supraoccipital crest, pterotic ridge, spine on the interopercle, other head spination, and a pigmentation pattern identical to Atlantic spadefish. Vertebral,

dorsal, and anal fin counts overlap between black driftfish and Atlantic spadefish, but teeth are found in a single band on the dentary in black driftfish (Ginsburg, 1954) and in two bands in Atlantic spadefish (Hildebrand and Cable, 1938; this study). Dawson's 5.7–7.9 mm specimens had teeth in two bands along the dentary. Because it is unlikely that black driftfish larvae have the same suite of characters as Atlantic spadefish, Dawson's specimens should be assigned to Atlantic spadefish.

Atlantic spadefish spawn from May through September based on seasonal abundance of Atlantic spadefish larvae in the northern Gulf; peak spawning occurs between June and August (Ditty et al., 1988; this study). Density estimates were highest during June in this study (Table 3), during July in a previous study of coastal waters off central Louisiana (Ditty, 1986), and during July and August off Mississippi Sound (Stuck and Perry, 1982). Neuston net collections were greatest during August (Table 3). Gonad maturity data off South Carolina support peak spawning of Atlantic spadefish during summer (Hayse, 1990).

Spatial distribution data indicate that Atlantic spadefish larvae are apparently rare in the eastern Gulf. Only one larva was collected east of Mobile Bay (Alabama) during this study, and one larva by Houde et al.[3] in a survey of Gulf waters off Florida. In addition, distribution of both larvae and station depths where larvae were collected indicates that Atlantic spadefish occur primarily in coastal waters (Ditty and Truesdale, 1984; this study), except near the Mississippi River delta where waters may offer additional habitat suitable to larvae because of lower salinities. The relatively high number of positive stations (26%) near the delta during August 1988 sampling of frontal zones suggests that frontal zones may concentrate larvae. Frontal zone waters may also provide a richer environment for feeding and growth of larvae because of higher phytoplankton and zooplankton biomass (Govoni et al., 1989; Grimes and Finucane, 1991). However, Powell et al. (1990) were unable to demonstrate consistently that larvae have a nutritional advantage when associated with the Mississippi River plume. A possible association of Atlantic spadefish larvae with riverine frontal areas requires further study.

In conclusion, understanding the biology, life history, and relations of Atlantic spadefish requires a knowledge of the morphology, distribution, and ecology of their larvae. Larval characters (e.g. degree of head spination) may also provide insight into the interrelationships among the Ephippidae and their relationship to other families. The potential use of larval characters in defining these relationships, however, cannot be clearly understood until larval development within the family is more fully documented (Watson and Walker, 1992).

[3] Houde, E. D., J. C. Leak, C. E. Dowd, S. A. Berkeley, and W. J. Richards. 1979. Ichthyoplankton abundance and diversity in the eastern Gulf of Mexico. Univ. Miami Report BLM Contract No. AA550-CT7-28, Miami, FL 33149, 546 p.

Acknowledgments

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Literature cited

Berry, F. H., and W. J. Richards.
1973. Characters useful to the study of larval fishes. Mid. Atl. Coast. Fish. Cent. Tech. Pap. 1:48–65.

Dawson, C. E.
1971. Notes on juvenile black driftfish, *Hyperoglyphe bythites*, from the northern Gulf of Mexico. Copeia 1971(4):732–735.

Ditty, J. G.
1986. Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana: composition, relative abundance, and seasonality. Fish. Bull. 84(4):935–946.

Ditty, J. G., and F. M. Truesdale.
1984. Ichthyoplankton surveys of nearshore Gulf waters off Louisiana: January–February and July 1976. Assoc. Southeastern Biol. Bull. 31(2):55–56.

Ditty, J. G., G. G. Zieske, and R. F. Shaw.
1988. Seasonality and depth distribution of larval fishes in the northern Gulf of Mexico above 26°00'N latitude. Fish. Bull. 86(4):811–823.

Ginsburg, I.
1954. Four new fishes and one little known species from the east coast of the United States, includ-

ing the Gulf of Mexico. J. Wash. Acad. Sci. 44:256–264.

Govoni, J. J., D. E. Hoss, and D. R. Colby.
1989. The spatial distribution of larval fishes about the Mississippi River plume. Limnol. Oceanogr. 34(1):178–187.

Gregory, W. K.
1933. Fish skulls: a study of the evolution of natural mechanisms. Trans. Am. Philos. Soc. 23:75–481.

Grimes, C. B., and J. H. Finucane.
1991. Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. Mar. Ecol. Prog. Ser. 75:109–119.

Hayse, J. W.
1990. Feeding habits, age, growth, and reproduction of Atlantic spadefish *Chaetodipterus faber* (Pisces: Ephippidae) in South Carolina. Fish. Bull. 88(1):67–83.

Hildebrand, S. F., and L. E. Cable.
1938. Further notes on the development and life history of some teleosts at Beaufort, N. C. Bull. U.S. Bur. Fish. 48(24):505–642.

Hubbs, C. L., and K. F. Lagler.
1958. The fishes of the Great Lakes region. Univ. Mich. Press, Ann Arbor, 213 p.

Johnson, G. D.
1978. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval, and juvenile stages. Vol. IV: Carangidae through Ephippidae. U.S. Fish. Wildl. Serv., Biol. Serv. Prog. FWS/OBS-78/12, 314 p.
1984. Percoidei: development and relationships. *In* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson (eds.), Ontogeny and systematics of fishes, p. 464–498. Am. Soc. Ichthy. Herp., Spec. Publ. No. 1.

Leis, J. M., and T. Trnski.
1989. The larvae of Indo-Pacific shorefishes. Univ. Hawaii Press, Honolulu, 371 p.

Martinez-Pecero, R., E. Matus-Nivon, R. Ramirez-Sevilla, D. E. Hernandez-Ceballos, and M. Contreras-Olguin.
1990. Huevo, larva y juvenil del peluquero *Chaetodipterus zonatus* (Girard) (Pisces: Ephippididae). Rev. Biol. Trop. 38(1):71–78. (In Spanish.)

Nelson, J. S.
1984. Fishes of the world, 2nd ed. John Wiley & Sons, NY, 523 p.

Powell, A. B., A. J. Chester, J. J. Govoni, and S. M. Warlen.
1990. Nutritional condition of spot larvae associated with the Mississippi River plume. Trans. Am. Fish. Soc. 119:957–965.

Richardson, S. L., and W. A. Laroche.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri, Sebastes pinniger*, and *Sebastes helvomaculatus* (family Scorpaenidae) off Oregon. Fish. Bull. 77(1):1–46.

Ryder, J. A.
1887. On the development of osseous fishes, including marine and freshwater forms. Rep. U.S. Fish. Comm., Part 13, 1885 (1887):489–604.

Sanders, N., Jr., T. Van Devender, and P. A. Thompson.
1990. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1986. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 20, 328 p.

SAS Institute, Inc.
1985. SAS User's Guide: statistics, 1985 ed. SAS Institute, Cary, NC, 584 p.

Schmied, R. L., and E. E. Burgess.
1987. Marine recreational fisheries in the southeastern United States: an overview. Mar. Fish. Rev. 49(2):1–7.

Smith, P. E., and S. L. Richardson.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Paper No. 175, 100 p.

Stuck, K. C., and H. M. Perry.
1982. Ichthyoplankton community structure in Mississippi coastal waters. *In* Fishery monitoring and assessment completion report, 1 January 1977 to 31 December 1981, p. VI-I-1 thru VI-I-53. Gulf Coast Res. Lab. (Ocean Springs, MS), Proj. No. 2-296-R.

Stuntz, W. E., C. E. Bryan, K. Savastano, R. S. Waller, and P. A. Thompson.
1985. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1982. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 12, 145 p.

Thompson, P. A., and N. Bane.
1986a. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1983. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 13, 179 p.
1986b. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1984. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 15, 171 p.

Thompson, P. A., T. Van Devender, and N. J. Sanders Jr.
1988. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1985. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 17, 338 p.

Watson, W., and H. J. Walker Jr.
1992. Larval development of sargo *(Anisotremus davidsonii)* and salema *(Xenistius californiensis)* (Pisces: Haemulidae) from the Southern California Bight. Bull. Mar. Sci. 51(3):360–406.

Appendix Table

Summary of total number of bongo net/neuston net stations examined for Atlantic spadefish larvae (*Chaetodipterus faber*) in the Gulf of Mexico. Acronyms are as follows: SEAMAP - Southeast Area Monitoring and Assessment Program; NMFS - National Marine Fisheries Service, Panama City, Florida. NS means no samples.

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
SEAMAP										
1982	77[1]/0[2]	69/68	71/73	102/100	26/24	NS	NS	3/8	29/3	NS
1983	15/13	27/27	84/84	55/45	44/42	NS	NS	39/26	NS	24/23
1984	23/0	44/0	46/0	55/54	20/26	155/162	NS	24/0	6/0	36/36
1985	29/0	NS	NS	85/0	39/0	69/0	20/0	4/0	2/0	24/0
1986	NS	24/0	90/0	57/0	10/0	NS	145/0	43/0	73/0	24/0
Total	144/13	164/95	291/157	354/199	139/92	224/162	165/0	113/34	110/3	108/59
NMFS[2]										
1988	55	71	36							

[1] 60-cm bongo net, 0.333-mm mesh, oblique-tow from depth.
[2] 1 × 2 m neuston net, 0.947-mm mesh, 10 min. surface-tow, unmetered.

Abstract.— Dolphinfishes are highly prized commercial and recreational species of worldwide distribution in tropical and subtropical seas, but the development and distribution of their larvae are poorly understood. Common dolphin eggs hatch in about 38 hours at 25°C based on a predictive relationship among egg diameter, water temperature, and development time. Morphometrics are generally greater in pompano dolphin than in common dolphin. Pompano dolphin are deeper–bodied and have a larger eye by 9 mm, and a larger mouth and longer pre-anal length by about 13 mm. Differences in pigment along the caudal peduncle and its finfold separate common dolphin from pompano dolphin <4.0–4.5 mm SL; common dolphin lack pigment in these areas. Number of spines along the outer shelf of the preopercle also separate species although preopercle spines are often difficult to count on larvae not cleared and stained; common dolphin have four spines along the outer preopercular shelf and pompano dolphin have five. Pigmented pelvic fins and bands of pigment laterally on both the body and median fins of common dolphin are diagnostic for separating species >8 mm SL; pompano dolphin lack these characters. Both common dolphin and pompano dolphin larvae usually are found at ≥24°C, ≥33 ppt, and beyond the 50 m isobath. Preflexion larvae (<7.0–7.5 mm SL) were primarily collected in oceanic waters. Both species may spawn year–round, at least in the southern part of the survey area. Larval common dolphin are significantly more abundant than pompano dolphin.

Larval development, distribution, and abundance of common dolphin, *Coryphaena hippurus*, and pompano dolphin, *C. equiselis* (family: Coryphaenidae), in the northern Gulf of Mexico*

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The dolphinfishes, *Coryphaena hippurus* (common dolphin) and *C. equiselis* (pompano dolphin), are distributed worldwide in tropical and subtropical seas (Briggs, 1960). Highly prized as food, these fishes are important recreational and commercial species, but relatively little is known about their early life stages. Gibbs and Collette (1959) reviewed spawning and adult seasonal distribution for the western North Atlantic Ocean, and Palko et al. (1982) compiled dolphinfish biological data. Aoki and Ueyanagi (1989) discussed larval and early juvenile distribution for the eastern Pacific, and similar information is available for the western Pacific and Indian oceans (Shcherbachev, 1973). Preliminary distribution maps are available for the Gulf of Mexico (Gulf), but associated environmental data are not included (Richards et al., 1984; Kelley et al., 1986). Embryonic development is described for common dolphin (Mito, 1960; Hassler and Rainville, 1975; Hagood and Rothwell[1]) and osteological development for both species (Potthoff, 1980), but descriptive larval morphology is primarily limited to sizes >13 mm SL (Gibbs and Collette, 1959; Shcherbachev, 1973). Okiyama (1988) and Aoki and Ueyanagi (1989) provide information on developmental morphology of Pacific specimens <13 mm SL, but their illustrations are

[1] Hagood, R. W., and G. N. Rothwell. 1979. Sea Grant interim project report—1979. Aquaculture in tropical ocean—*Coryphaena* sp. Oceanic Inst., Makapuu Point, Waimanalo, HI 96795.

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insufficient to examine important details, and Okiyama's study is a general overview of exisitng information. The utility of early life stages of *Coryphaena* in examining previous phylogenetic hypotheses and evolutionary interrelationships of echeneoids (i.e. Coryphaenidae-Rachycentridae-Echeneididae) is discussed by Johnson (1984). Our objectives are 1) to describe and compare early larval development of common dolphin and pompano dolphin using the dynamic approach to larval description (Berry and Richards, 1973) and 2) to describe the spatial and temporal distribution and abundance of early life stages of dolphinfishes in the northern Gulf.

Materials and methods

Seasonal occurrence, distribution, and abundance of dolphinfish larvae were determined primarily from 814 neuston net collections taken during Southeast Area Monitoring and Assessment Program (SEAMAP) ichthyoplankton surveys of the Gulf between 1982 and 1984 (1982–276 stations, 1983–260, 1984–278). These years represent the first time interval for which a complete set of data was currently available. SEAMAP collections were made with an unmetered 1×2 m net (0.947-mm mesh) towed at the surface for 10 minutes at each station. The SEAMAP effort also involved the collection and processing of about 1,819 bongo net stations between 1982 and 1986 (1982–384 stations, 1983–288, 1984–409, 1985–272, and 1986–466) (SEAMAP 1983–1987)[2]. Bongo nets (60-cm net, 0.333-mm mesh) were towed obliquely to the surface from within 5 m of the bottom or from a maximum depth of 200 m. Sampling during April and May was primarily beyond the continental shelf, and that during March and from June to November was primarily over the shelf at stations <180 m depth. No samples were taken during January and February. Tows were made during both day and night depending on when the ship occupied the station. Latitude 24°30'N was the southern boundary of our survey area in the eastern Gulf and latitude 26°00'N the southern boundary of the central and western Gulf (Appendix Fig. 1). These coordinates approximate the U.S. Exclusive Economic Zone (EEZ)/Fishery Conservation Zone (FCZ). Additional information on temporal and spatial coverage of SEAMAP plankton surveys are found in Stuntz et al. (1985), Thompson and Bane (1986, a and b), Thompson et al. (1988), and Sanders et al. (1990).

Ichthyoplankton collections were also examined from riverine/oceanic frontal zones off the Mississippi River delta. These collections were from surface-towed 1×2 m neuston nets (0.947-mm mesh, 10–min. tows, sample n=311) and were obtained from the National Marine Fisheries Service (NMFS), Panama City, Florida (i.e. May 1988 [55 neuston samples]; August 1988 [71]; September 1986 [46], 1987 [68], and 1989 [35]; and December 1988 [36]).

A detailed examination of dolphinfish larvae was made to describe developmental morphology. We examined 25 common dolphin and 19 pompano dolphin larvae between 3.5 and 15.0 mm SL for differences in pigmentation, developmental morphology, and head spination, but only cursorily discuss fin development because of a thorough review of these structures by Potthoff (1980). Body measurements were made to the nearest 0.1 mm with a dissecting scope and ocular micrometer following Hubbs and Lagler (1958) and Richardson and Laroche (1979). We follow Leis and Trnski's (1989) criteria for defining length of preopercular spines, body depth, head length, and eye diameter. We consider notochord length in preflexion and flexion larvae synonymous with standard length (SL) in postflexion larvae and report all lengths as SL unless otherwise noted. Specimens were field-fixed in 10% formalin and later transferred to 70% ethyl alcohol. We used a compound scope to examine origin and location of epithelial spicules and the maxillary spine. Juveniles are those >25 mm, when specimens usually have developed a full complement of rays in all fins and scales (Johnson, 1984). Representative specimens were illustrated with a camera lucida (Figs. 1 and 2). Only three pompano dolphin <4 mm were collected and these were in too poor a condition to illustrate.

Estimates of larval catch (number of larvae/neuston tow) were calculated for each station. Mean catch estimates by month and season were calculated by dividing the sum of larvae (by species) by the total number of stations sampled within each category (month, season, etc.) and multiplying the result by 10 (number of larvae/10 neuston tows). Mean catch more closely reflects the abundance of larvae throughout the area by including total sampling effort in calculations. Catch was combined by month and by season across years. Seasons were defined as follows: spring=March to May; summer=June to August; and fall=September to November (Appendix Fig. 2).

Nonparametric tests were used to evaluate diel, seasonal, and overall differences in catch of common

[2] SEAMAP. 1983–1987. (plankton). ASCII characters. Data for 1982–1986. Fisheries-independent survey data/National Marine Fisheries Service, Southeast Fisheries Center: Gulf States Marine Fisheries Commission, Ocean Springs, MS (producer).

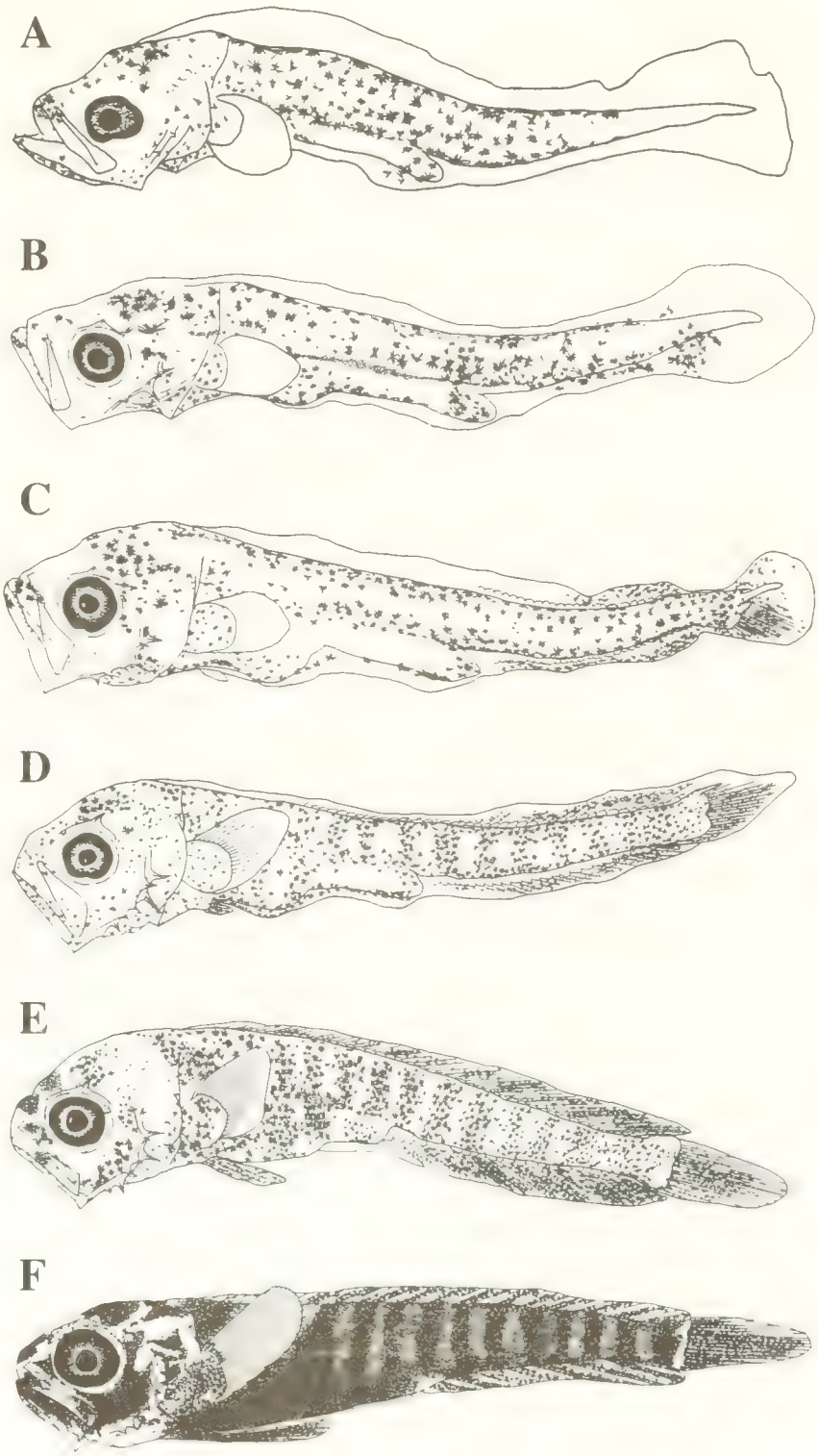

Figure 1

Larval development of common dolphin (*Coryphaena hippurus*) from the northern Gulf of Mexico. (**A**) 3.5 mm, (**B**) 5.0 mm, (**C**) 7.1 mm, (**D**) 9.5 mm, (**E**) 11.0 mm, (**F**) 14.0 mm. All measurements are in standard length (SL).

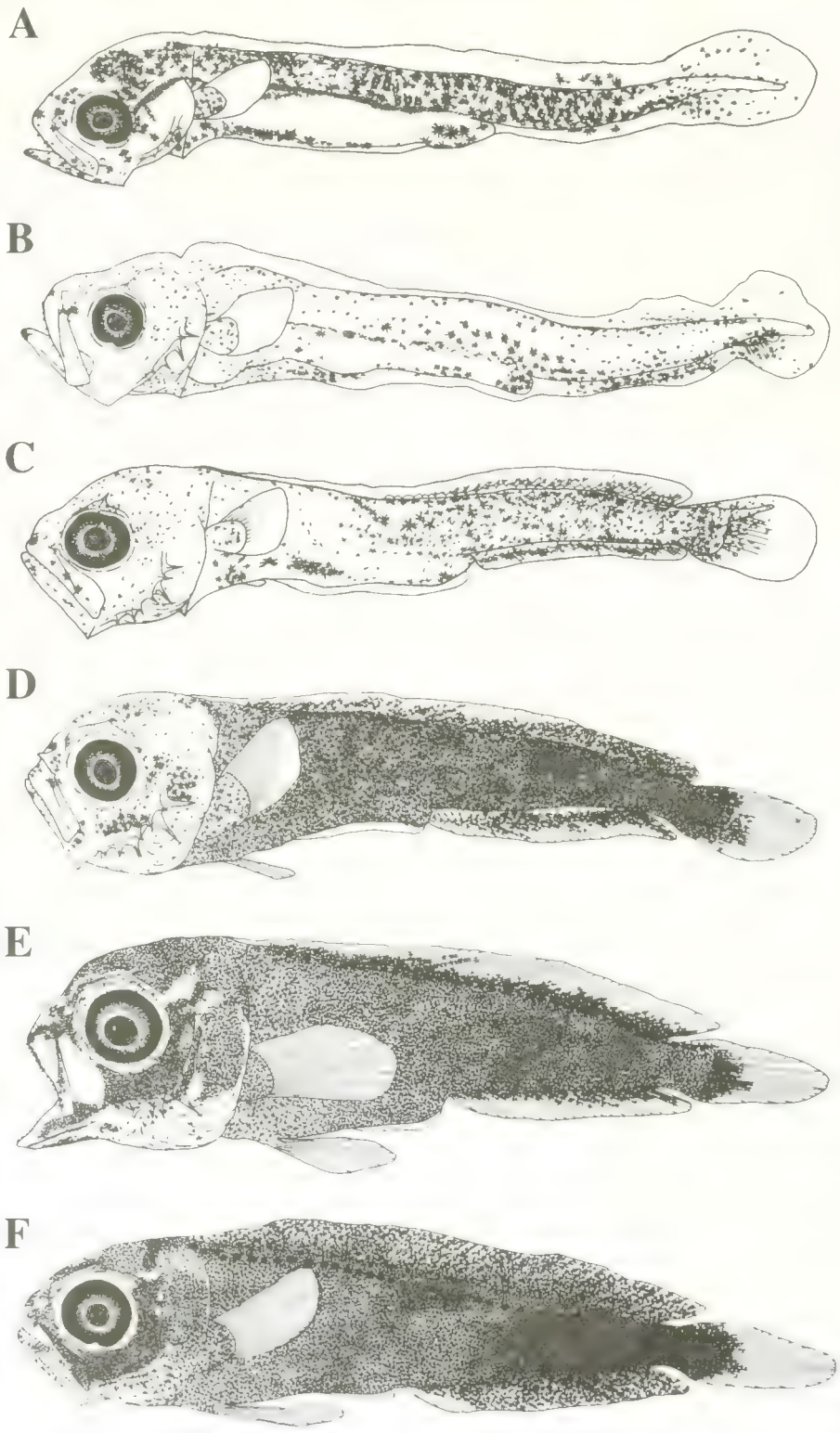

Figure 2

Larval development of pompano dolphin (*Coryphaena equiselis*) from the northern Gulf of Mexico. (**A**) 4.7 mm, (**B**) 5.5 mm, (**C**) 7.5 mm, (**D**) 9.7 mm, (**E**) 11.5 mm, (**F**) 15.0 mm. All measurements are in standard length (SL).

dolphin and pompano dolphin. Only those stations where either of the two species were present were included in analyses. A Kruskal-Wallis test was used to detect differences among groups (α=0.05) and a Tukey-type test to determine if mean differences were significant (Zar, 1984; SAS Institute, 1985). Dolphinfish >25 mm were excluded from analyses.

Temperature and salinity data were taken from the sea surface only. Hydrographic data were multiplied by number of larvae caught (by species) at each station to obtain an overall median and mean. This method gives weight to distribution of larvae rather than distribution of stations. We used a percent cumulative frequency of ≥75% for determining the relationship between distribution of dolphinfish larvae and surface water temperature, salinity, and station depth. Percent frequency indicates the range of hydrographic conditions most often associated with occurrences of larvae. Proc Univariate was used to calculate median, mean, and percent cumulative frequency statistics (SAS Institute, 1985). We divided the continental shelf into approximately equal geographic areas (i.e. into sq. km.) based on depth and designated the inner shelf as <50 m deep, outer shelf waters as those from 50 to 180 m deep, and oceanic waters as those beyond the continental shelf (i.e. >180 m).

Results

Morphology

A continuous median finfold extended posteriorly along the body of early larvae of both species from the posterior midbrain to the cleithral symphysis. Remnants of the finfold were visible ventrally along the hindgut (i.e. preanal finfold) at least through 15 mm. Minute epithelial spicules covered the body of each species by 4 mm and were best observed on the head and larval finfold. Spicules were more easily observed as larvae grew. Yolk-sac larvae <3.5 mm of common dolphin and pompano dolphin had unpigmented eyes. Preflexion larvae (<7.0–7.5 mm) of both species were elongate, with body depth usually ≤20% SL. The body became relatively deeper during flexion (about 7.5–9.0 mm) and pompano dolphin were deeper-bodied than were common dolphin by early postflexion (Table 1). The head was moderately long (i.e. between 20 and 33% SL) in both species and the snout was short and blunt. The eyes were round and larger in pompano dolphin than in common dolphin by early postflexion (Table 1). The mouth was large and oblique; upper jaw length usually ranged from 42 to 45% of head length in postflexion dolphinfish of both species. Pompano dolphin have a larger mouth than do common dolphin by 13 mm (Table 1). The foregut was partially convoluted and had a half-twist in preflexion larvae of both species and a single loop in larger larvae; the hindgut was straight. By 13 mm, however, preanal length was generally greater in pompano dolphin than in common dolphin (Table 1). Preanal length usually ranged from 60 to 65% SL during preflexion, but decreased thereafter to 55–60% SL in both species. The pelvic fins were moderately long (about 15–18% SL; Table 1) and extend to the tips of the pectorals by 12 mm. Myomeres were obscured by heavy

Table 1

Morphometrics of larval common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) from the northern Gulf of Mexico. Measurements are expressed as % standard length (SL).

SL (mm)	*N*	Preanal length	Head length	Snout length	Orbit diameter	Upper jaw length	Body depth cleithrum	Prepelvic distance	Pelvic length
C. hippurus									
3.5–4.9	5	57.0–65.0	23.0–25.0	4.0–6.0	9.0–10.0	11.0–12.5	16.5–18.5		
5.0–6.9	4	61.0–65.0	24.0–27.0	5.0–6.0	8.0–9.5	9.0–13.0	17.0–22.0	31.0–34.0	bud
7.0–8.9	4	60.0–63.0	23.0–27.0	5.0–6.0	7.0–9.0	9.5–12.0	16.0–20.0	27.0–32.5	bud–3.0
9.0–10.9	3	56.0–59.0	25.0–28.0	5.5–6.0	9.5–11.0	12.0–13.0	19.0–21.0	27.0–30.0	4.5–11.0
11.0–12.9	5	54.0–57.0	24.0–27.0	5.0–6.0	10.0–11.0	11.0–13.0	20.0–23.0	27.0–28.0	11.0–15.0
13.0–14.9	4	54.0–56.5	25.0–28.0	4.0–5.0	11.0–11.5	12.0–12.5	21.0–22.5	26.0–30.0	17.0–18.5
C. equiselis									
3.7–4.9	3	60.0–65.0	23.0–27.5	5.0–6.0	9.5–10.0	11.5–13.0	19.0–21.0	—	—
5.0–6.1	4	60.0–62.0	23.0–24.0	5.0–6.0	8.5–10.0	10.0–13.0	16.0–20.0	—	–
7.5–8.9	2	46.0–47.0	19.0–22.0	4.0–4.5	8.0–9.5	10.0–12.0	16.0–22.0	22.0–24.0	bud–6.0
9.0–10.9	3	56.0–60.0	27.0–30.0	4.5–5.0	12.0–12.0	12.0–15.0	25.0–29.0	30.0–35.0	8.5–14.0
11.0–12.9	4	55.0–60.0	25.0–30.0	4.0–5.0	12.0–14.0	12.0–14.0	27.0–29.0	31.0–35.0	13.0–15.0
13.0–15.0	3	55.0–60.0	27.0–30.0	4.0–5.0	13.0–13.0	13.0–15.0	25.5–28.0	28.0–34.0	16.0–18.5

pigmentation and were difficult to count on dolphinfish larvae; however, a 5.5-mm pompano dolphin had 33 myomeres and a partially cleared 11-mm common dolphin had 30 vertebrae. Only two pompano dolphin between 6.1 and 9.7 mm were collected (7.5 and 8.5 mm) and morphometrics for these larvae were considerably smaller than for the other specimens (Table 1).

Pigmentation

Dolphinfish were heavily pigmented at all sizes, except the caudal peduncle and its finfold in early preflexion larvae of common dolphin which was unpigmented (Fig. 1). In common dolphin <4 mm, the length of the unpigmented portion of the caudal peduncle was 15–20% SL. By 4.5–5.0 mm, however, pigment was present along the caudal peduncle and on the caudal finfold (Fig. 1). Early preflexion pompano dolphin <4 mm had a row of melanophores along the caudal peduncle (both dorsally and ventrally) and pigment was scattered throughout the caudal finfold (Fig. 2). On the head, pigment was scattered externally over the premaxilla, snout, and fore-, mid-, and hind-brain of early larvae of each species. Pigment also was present along the dentary, lower jaw, isthmus, branchiostegal rays, and on the roof of the mouth. On the visceral mass, melanophores were scattered over the foregut and anus of early preflexion larvae of both species but the hindgut was sparsely pigmented laterally (Figs. 1 and 2). Gut pigmentation increased with length. Vertical bands of pigment first formed along the dorsal and anal fins of common dolphin at about 8 mm. These bands of pigment subsequently extended across the body; 12 to 13 poorly formed bands were visible by 10 mm. Vertical bands became more distinct as larvae grew (Fig. 1). Bands of pigment do not form in pompano dolphin, but this species does have a row of enlarged melanophores along the body dorso- and ventro-laterally (adjacent to the dorsal and anal fin bases) by 7.5 mm, which was not present in common dolphin (Figs. 1 and 2).

Pectoral buds were present on early larvae of each species. Pigment was scattered over the pectoral axilla and was heavier on pompano dolphin than on common dolphin of similar length. The proximal portion of the upper pectoral rays of common dolphin was pigmented by 14–15 mm; no pigment was present on the pectoral rays of pompano dolphin. Dorsal- and anal-fin bases were thickening by 5 mm in pompano dolphin and by 6 mm in common dolphin; the anal-fin base developed slightly before that of the dorsal base. Both fin bases and their ray anlagen developed in a posterior to anterior direction. Pelvic-fin buds of common dolphin were present by 6.5 mm and pigmented by 7.5 mm. No pompano dolphin between 6.1 and 7.5 mm were examined, but the pelvic buds were present by 7.5 mm. The pelvic rays of pompano dolphin remained unpigmented at all sizes. Pigment occurred on the developing caudal rays of each species by early flexion. By 10 mm, all but the distal tips of the caudal rays were pigmented in common dolphin; only about the proximal third of each caudal ray was pigmented in pompano dolphin. Differences in caudal-fin pigmentation were more pronounced as larvae grew (Figs. 1 and 2).

Head and body spination

Dolphinfish larvae developed two series of preopercle spines, one series along the posterior margin of the inner shelf and the other along the outer shelf. Number and location of spines along the outer shelf of the preopercle separate larval common dolphin from pompano dolphin. Two spines were present along the margin of both the inner and outer preopercular shelves of 4-mm common dolphin, the largest spines occurring on either side of the angle of the preopercle (Figs. 1 and 2). A third spine was added along both the inner and outer shelf by 7 mm; a fourth spine was added along the outer preopercle by 10.0–10.5 mm. A total of three spines occurred along the inner and four spines along the outer shelf of the preopercle of larval common dolphin (Fig. 1). Arrangement of preopercle spines in larval pompano dolphin <4 mm was similar to that in common dolphin except three rather than two spines were visible along the outer preopercular shelf. A third spine was added along the inner shelf by 7 mm and a fourth and fifth spine along the outer shelf by 9 mm. A total of three spines occurred along the inner and five spines along the outer preopercular shelf of larval pompano dolphin (Fig. 2). Number and placement of preopercle spines were consistent through at least 15 mm in both species. All preopercle spines were simple (Figs. 1 and 2).

Dolphinfish have several spines and ridges on the head. The pterotic area was swollen in both species by 5 mm and a laterally directed spine was present along the supraorbital ridge of each frontal bone of 6-mm pompano dolphin and 7-mm common dolphin (Figs. 1 and 2). The supraorbital ridge of each species usually had a single spine, but some pompano dolphin had two or three spines along the ridge. The swollen pterotics and supraorbital spine were best observed when specimens were viewed dorsally; both features were well developed by 7.5–8.0 mm. The frontal bone was notably thicker above the eye of pompano dolphin, but the supraorbital ridge was less well developed in pompano dolphin than in common dolphin by 9.5 mm. The supraorbital spine(s)

of pompano dolphin were regressing by 11–12 mm. A small spine was present anteriorly along the maxilla of each species by 5 mm (Figs. 1 and 2). The maxillary spine (difficult to locate because of its position and size) pointed dorso-laterally and was slightly better developed in pompano dolphin than in common dolphin of similar size. A posttemporal spine was present in both species by 9 mm and was most easily observed when specimens were viewed dorsally. The anterior portion of the lacrimal bone was prominent in dolphinfish larvae; the lacrimal was more pronounced in pompano than in common dolphin by late flexion (Figs. 1D and 2D).

Minute teeth were present anteriorly on the upper and lower jaws of each species by 3.8 mm. Number and size of teeth increased with SL. A pair of canine-like teeth were present in 10-mm pompano dolphin and 11-mm common dolphin.

Spatial and temporal distribution

Larval dolphinfish were collected during all months sampled, but small larvae of both species were found primarily during warm months. Preflexion larvae of common dolphin occurred mainly from April through November. One common dolphin larva (7.0 mm) was also collected during December (21, 1983), at a station due south of Caminada Pass, Louisiana (23.5°C, station depth: 531 m). Larval pompano dolphin were collected from March through October; larvae <10 mm were collected through late September. Only one pompano dolphin larva (5 mm) was collected during March (13, 1982; water temperature: 18°C), at a bongo-net station 29 m deep off Caminada Pass, Louisiana. Two pompano dolphin larvae (18.3 and 22.5 mm) were collected during October (14 and 17, 1983), but they were probably spawned during late September.

Larvae of common dolphin and pompano dolphin were collected primarily at water temperatures ≥24°C (90% of larvae) and salinities ≥33 ppt (≥75%) (Table 2, Fig. 3). The pompano dolphin collected during March was the only larva of either species taken at <21°C. Based on water temperatures when common dolphin larvae usually occurred (≥24°C) and using Pauly and Pullin's (1988) relationship between egg diameter and water temperature to predict development time in other marine fishes, we estimate a common dolphin egg of 1.4 mean-mm diameter would hatch in about 38 hours at 25°C and 26 hours at 30°C (Table 3). Few common dolphin larvae and no pompano dolphin were collected at <25 ppt (Table 2; Fig. 3).

Larval dolphinfish of both species were widely distributed in neritic and oceanic waters of the Gulf and most were collected near the surface. Over 90% of common dolphin and about 80% of pompano dolphin occurred over the outer continental shelf and in oceanic waters; preflexion larvae were usually taken in oceanic waters (stations >180 m deep) (Appendix Fig. 3). Overall, larval common dolphin were significantly more abundant than pompano dolphin (Kruskal-Wallis, $P \leq 0.0001$, df= 362; Table 4). Larval common dolphin were also collected at more stations than were pompano dolphin (15.0% versus 5.1% of all stations sampled, respectively; Table 4). Only 3.1% of oblique bongo-net samples (1982–86, n=1819) took common dolphin larvae (no. larvae=83, length=6.5 mm, range=3.2–21.8 mm) and <0.01% captured pompano dolphin (no. larvae=10, $\bar{x}$ length=4.6 mm, range=4.0–8.7 mm).

Differences in catch of common dolphin and pompano dolphin, respectively, were not significant among seasons or between day and night. About 25% of spring and 18% of fall neuston stations collected larval common dolphin, but <9% of those stations sampled during summer (Table 4). Larval pompano dolphin were collected at 7% of spring neuston stations, 2% of summer stations, and 8% of fall stations (Table 4). Only two neuston tows collected >13 larvae of either species; these two tows ac-

Table 2

Summary of hydrographic data for common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) larvae collected in the northern Gulf of Mexico. Data are from the sea surface only; median values are obtained from the distribution of larvae versus the hydrographic parameter. Bongo and neuston net data are combined. '*N*' is number of larvae used in obtaining median values. Discrepancies in '*N*' result from missing values in the hydrographic data.

	Salinity (ppt)			Water temperature (°C)			Station depth (m)		
	N	Median	Range	*N*	Median	Range	*N*	Median	Range
C. hippurus	537	34.0	18.7–37.8	590	28.0	21.4–32.0	599	195	11–3475
C. equiselis	80	35.1	25.0–37.8	94	27.6	18.0–30.4	94	195	11–3325

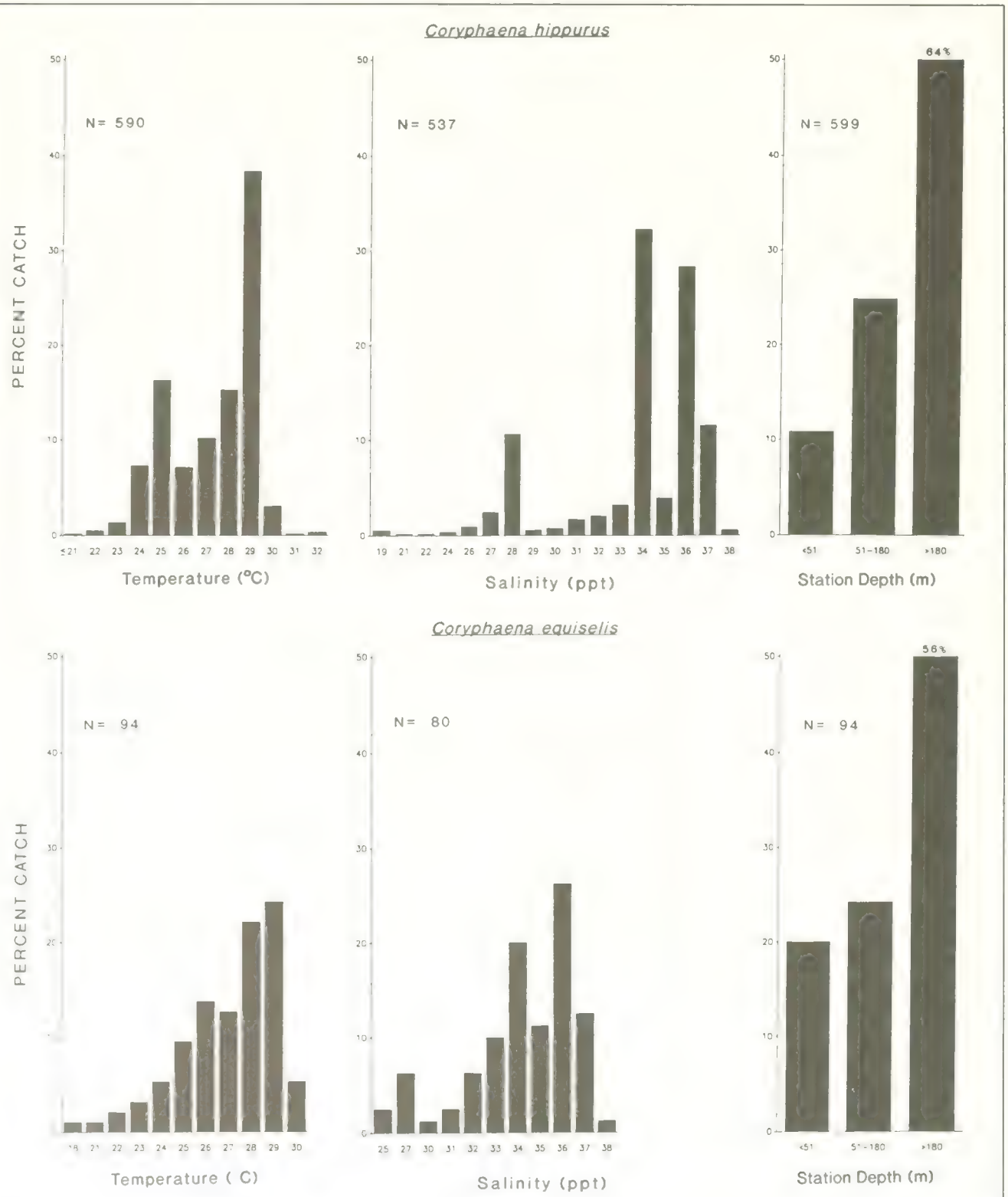

Figure 3

Summary of hydrographic data for larval common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) in the northern Gulf of Mexico. Data are from both bongo and neuston net tows. Hydrographic values are rounded to the nearest whole number. *N* = number of larvae. Discrepancies in *N* among parameters are the result of missing hydrographic data.

Table 3

Egg development time and hatching length (total length:TL) of common dolphin (*Coryphaena hippurus*).

Author	Egg diameter	°C	Hatching Time (hr)	Hatching TL (mm)	Study location
Mito, 1960	1.28–1.62	21–29	48–60	3.95	Japan
Hassler and Rainville, 1975	1.3[1]	27[1]	—	3.0[2]	Atlantic
Hagood and Rothwell	—	26	40	—	Hawaii
(see Footnote 1)	1.35[3]	26[3]	38[3]	—	Hawaii
Soichi, 1978	1.4–1.65	24–25	60	3.8–4.9[2]	Japan
Uchiyama et al., 1986	—	24–25	48–50	4.0–4.6	Hawaii
Lamadrid-Rose and Boehlert, 1988	1.52–1.66	26	54	4.3–5.4[4]	Hawaii
This study	1.4[5]	20	58[5]	—	Gulf of Mexico
		25	38[5]	—	
		30	26[5]	—	

[1] Mean.
[2] One-day-old larva.
[3] *C. equiselis*.
[4] Standard length.
[5] Mean egg diameter and predicted hatching times.

Table 4

Mean catch (no.larvae/10 neuston tows) of common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) larvae in the northern Gulf of Mexico by month. Collections for 1982–1984 are throughout the Gulf and those from 1986 to 1989 are primarily around the Mississippi River delta. Mean catch is calculated over all stations sampled by month; months are combined across years. Grand mean catch per 10 tows is calculated by dividing total number of larvae collected by all stations sampled. Numbers in parenthesis are positive catch stations over total stations sampled.

Taxa	N[1]	March	April	May	June	July	August	September	October	November	Grand Total
C. hippurus	517	0.0 (0/13)	3.4 (22/100)	7.6 (58/221)	2.9 (29/208)	0.5 (3/92)	0.5 (13/248)	13.4 (29/163)	3.9 (4/33)	16.7 (2/3)	4.8 (60/1081)
C. equiselis	85	0.8 (1/13)	1.2 (10/100)	0.9 (15/221)	1.0 (8/208)	0.2 (2/92)	<0.1 (1/248)	1.8 (16/163)	0.6 (2/33)	0.0 (0/3)	0.8 (54/1081)

[1] Number of larvae.

counted for about 40% of all common dolphin larvae taken. Both collections occurred off the Mississippi River delta, one during September 1986 (n=161, 195 m station depth) and the other during May 1988 (n=52, 63 m station depth).

Discussion

Early preflexion larvae (<4.0–4.5 mm) of pompano dolphin are separated from those of common dolphin by having melanophores along the caudal peduncle and scattered throughout the caudal finfold (Figs. 1 and 2). Number and placement of spines along the outer shelf of the preopercle also separate species (Table 5). Separation of dolphinfishes is particularly difficult between 4.5 and 8.0 mm because preopercle spines are often difficult to count on larvae not cleared and stained. At >8 mm, common dolphin are more easily separated from pompano dolphin by having pigment on the developing pelvic fins and bands of pigment laterally on the body and median fins (Figs. 1 and 2; Table 5). Differences in caudal-fin pigmentation also separate species by early

Table 5

Characters helpful in separating larvae of common dolphin (*Coryphaena hippurus*) from pompano dolphin (*C. equiselis*).

Species	Pigment			Outer preopercle spines	Meristics	
	Caudal peduncle	Pelvic fins	Vertical bands		Number of vertebrae	Dorsal fin rays
C. hippurus	Absent	Present[2]	Present[2, 3]	4	30–31	58–66
C. equiselis	Present[1]	Absent	Absent	5	33–44	52–59

[1] At <4.0–4.5 mm SL.
[2] At about 8.0 mm SL.
[3] Laterally on body and median fins.

postflexion (Figs. 1 and 2). In general, our findings agree with those of Aoki and Ueyanagi (1989). Lack of pelvic-fin pigment in pompano dolphin is diagnostic for separating the two species when common dolphin lose lateral banding through preservation or specimen deterioration. Although the 8.5-mm common dolphin larva illustrated in Johnson (1984) lacks pelvic pigment, this specimen has bands of pigment laterally on both the body and median fins.

Number of myomeres and dorsal-fin rays separate juvenile and adult common dolphin from pompano dolphin (30 or 31 vertebrae and 58–66 [$\bar{x}$=61] dorsal rays in common dolphin; 33 or 34 vertebrae and 52–59 [$\bar{x}$=55] dorsal rays in pompano dolphin; Collette et al., 1969; Potthoff, 1980). Great care must be taken when counting the most anterior dorsal-fin elements (Gibbs and Collette, 1959), however, because anterior dorsal rays are short and develop late (Potthoff, 1980). Myomeres are difficult to count without clearing and staining larvae because dolphinfish are heavily pigmented.

Early larval development of common dolphin and pompano dolphin from the Gulf is similar to that in the western Pacific Ocean (Aoki and Ueyanagi, 1989). Developmental milestones (e.g. initial formation of dorsal- and anal-fin bases, yolk-sac absorption, and lateral body banding) occur at similar sizes in common dolphin from both the Gulf and western Pacific Ocean. We found yolk-sac absorption in common dolphin complete by about 3.7 mm, as did Aoki and Ueyanagi (1989). Off Japan, however, common dolphin do not complete yolk-sac absorption until about 6 mm TL (Okiyama, 1988). Aoki and Ueyanagi (1989) did not discuss either maxillary or posttemporal spines or the epithelial spicules noted during this study.

Morphometrics are generally greater in pompano dolphin than in common dolphin from the gulf by early postflexion (Table 1). Differences in mean morphometric ratios (expressed as % SL) between species from the Pacific Ocean are significant (Student's *t*-test, α=0.05) for larvae 5–10 mm; relative growth of all body parts measured (except preanal length) were greater in pompano dolphin than in common dolphin (Aoki and Ueyanagi, 1989).

Distribution of dolphinfish larvae (Table 2, Fig. 3), juveniles, and adults is apparently limited by the 20°C isotherm (Gibbs and Collette, 1959). We found larval dolphinfish of both species primarily at temperatures ≥24°C and salinities ≥33 ppt, as did Fahay (1975), Powles (1981), and Aoki and Ueyanagi (1989). On the basis of water temperatures between 25 and 30°C (those when common dolphin larvae primarily occur), we estimate a common dolphin egg would hatch between 26 and 38 hours. Incubation time at 25°C predicted for common dolphin eggs from the Gulf was similar to that of Hagood and Rothwell[1] at 26°C, but less than incubation times predicted by other studies (Table 3).

Location of dolphinfish spawning is poorly documented. We believe that spawning occurs in oceanic waters based on the collection of preflexion larvae of both species at stations primarily beyond the continental shelf (Appendix Fig. 3). In addition, >80% of larvae of each species (Fig. 3) and 85% of stations where larvae occurred were over or beyond the outer continental shelf (Appendix Fig. 2). These findings support information from along the Atlantic coast of the southeastern U. S. that dolphinfish larvae are most abundant near or beyond the 180 m depth contour (Powles, 1981). In the Gulf, larvae of both common and pompano dolphin were collected over a similar median (Table 2), mean, and range of station depths (mean: 815 m for common dolphin and 782 m for pompano dolphin based on our weighted method of calculating these statistics). This similarity between species in distribution of larvae is reinforced by the average depth of stations where larvae were captured. Average station depth of capture was 1198 m for common dolphin (n=216 stations) and 1042 m for pompano dolphin (n=64 stations).

Other studies suggest that common dolphin in the tropical Atlantic (Gibbs and Collette, 1959) and Pacific (Aoki and Ueyanagi, 1989) spawn closer to shore than do pompano dolphin. In the Pacific, mid-oceanic occurrences of common dolphin larvae are limited to waters near islands (Aoki and Ueyanagi, 1989).

Overall, larval common dolphin are significantly more abundant than pompano dolphin in the northern Gulf (Table 4; Appendix Fig. 2) and along the southeastern United States (Fahay, 1975; Powles, 1981). Larvae of both common dolphin and pompano dolphin were particularly abundant around the Mississippi River delta. Higher larval dolphinfish abundances near the delta may reflect the generally higher abundance of fish larvae in the delta area (Ditty, 1986; Govoni et al., 1989; Grimes and Finucane, 1991) as compared to the open Gulf (Richards et al., 1989), or may reflect greater intensity of neuston sampling near the delta rather than the actual distribution of spawning adults. In the Pacific and Indian Oceans, larval pompano dolphin are more abundant than common dolphin (Shcherbachev, 1973; Aoki and Ueyanagi, 1989).

Dolphinfish may spawn year-round in the Gulf, at least in the southern part of the study area where seasonal water temperatures remain above about 24°C. Estimated spawning dates based on collection of preflexion common dolphin support spawning in the northern Gulf from at least April to December (Fig. 4). Peak spawning of common dolphin occurs during spring and early fall based on higher catches of larvae during these seasons, although differences among seasons are not significant. Along the Atlantic coast, eggs have been collected during July and August in the Gulf Stream (Hassler and Rainville, 1975) and larvae and early juveniles year-round along the southeastern United States (Fahay, 1975; Powles and Stender, 1976) and tropical Atlantic (Gibbs and Collette, 1959). Ripe female common dolphin occur in the Gulf Stream off Cape Hatteras (North Carolina) from at least May through July (Schuck, 1951; Rose, 1966), and in the Florida Current from November to July (March spawning peak, Beardsley, 1967). Pompano dolphin spawn in the Gulf from spring through at least early fall (Fig. 4; Gibbs and Collette, 1959). If larval pompano dolphin growth rates are similar to those for common dolphin (about 1 mm/day, Hassler and Rainville, 1975; Uchiyama et al., 1986), the two mid-October collected pompano dolphin larvae (18.3 and 22.5 mm) were spawned during late September. Pompano dolphin spawn year-round in tropical mid-Atlantic and South Atlantic Bight waters based on collection of larvae and juvenile length-frequency data (Potthoff, 1971; Fahay, 1975).

We found no significant diel differences in catch of larvae for either species as did Fahay (1975). Eldridge et al. (1977), however, found both common dolphin and pompano dolphin significantly more abundant at night, and that catch of larval common dolphin increased with concentration of *Sargassum*. Larval common dolphin <10 mm are more common in subsurface (i.e. depths of 20–30 m) than in surface tows during both day and night (Aoki and Ueyanagi, 1989). Larval pompano dolphin <10 mm are more frequently collected in subsurface tows during the day only; larvae >10 mm are more common near the surface during the night (Aoki and Ueyanagi, 1989).

New information on the larval morphology of pompano dolphin from this study corroborates Johnson's (1984) hypothesis of a relationship between Coryphaenidae and Rachycentridae rather than that previously hypothesized between Rachycentridae and Echeneididae. Larvae of dolphinfishes and cobia share similar patterns of head spination: laterally swollen pterotics; a single, simple spine on the supraorbital ridge of each frontal bone (except in *C. equiselis* which may have multiple spines along the ridge); a small posttemporal spine; and both dolphinfish and cobia have 3 or 4 spines along the inner shelf and 4 or 5 spines along the outer shelf of the preopercle with the largest spines on either side of the preopercular angle (Johnson, 1984; Ditty and Shaw, 1992; this study). Dolphinfishes have a small maxillary spine that cobia lack (Ditty and Shaw, 1992; this study), but no spine on the supracleithrum found in cobia (Dawson, 1971; Ditty and Shaw, 1992; this study). *Echeneis* lack head spines. Larval dolphinfishes and cobia also lack large hooked teeth anteriorly on the dentary found in *Echeneis* (Johnson, 1984; Leis and Trnski, 1989). Dolphinfishes differ from cobia by lacking dorsal and anal spines and by having more vertebrae (30–34 in dolphinfishes versus 25 in cobia). Dolphinfishes also have 50+ soft dorsal rays, whereas cobia have 27–33 (Ditty and Shaw, 1992).

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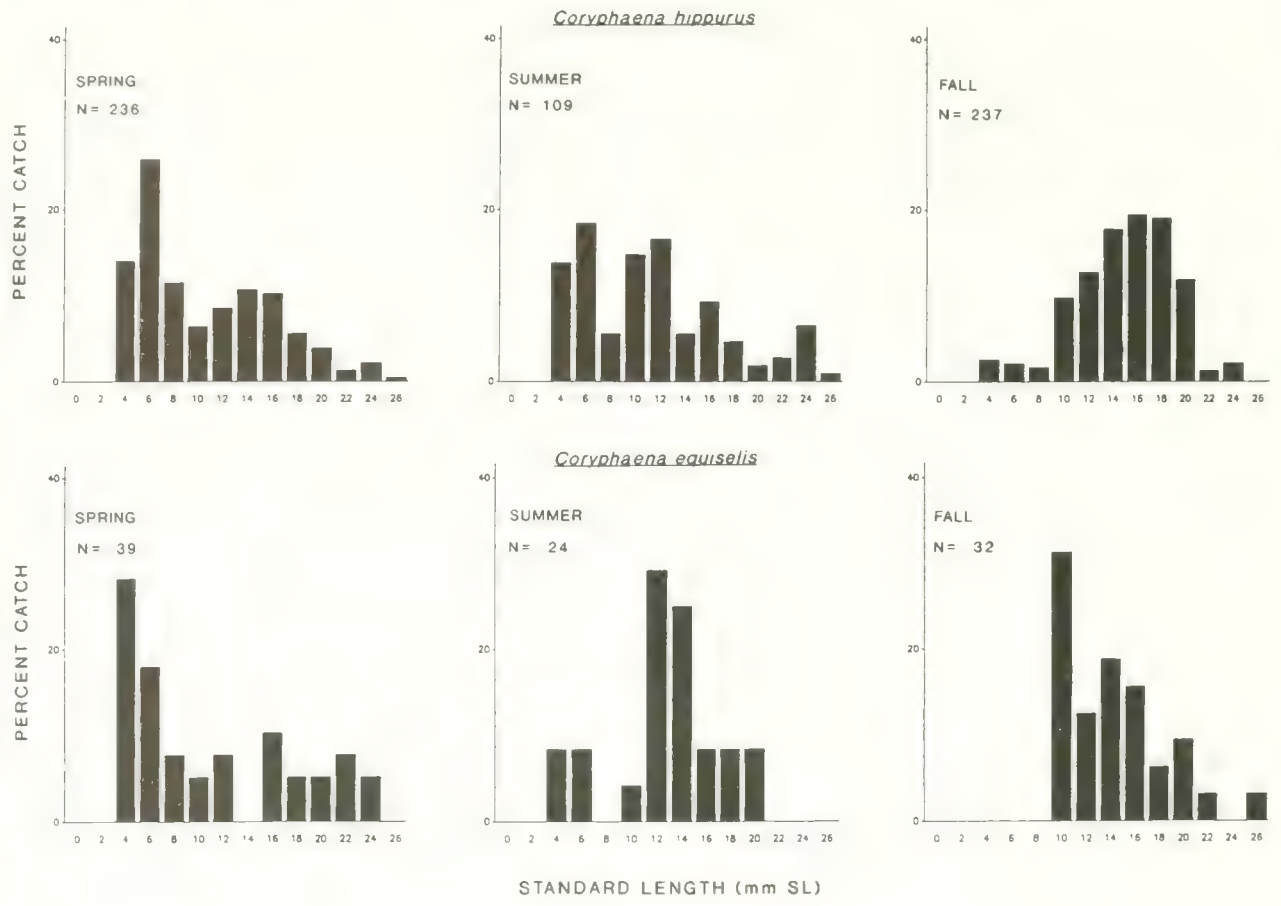


Figure 4

Length-frequency distribution of larval common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) in the northern Gulf of Mexico by season. Catches are from both bongo and neuston net tows; seasons are combined across years. Spring: March–May, Summer: June–August, Fall: September–November. Length categories are combined by 2-mm intervals; ≥0.5–mm increments are rounded to the nearest whole number. *N* = number of larvae.

copy of the English translation of Aoki and Ueyanagi (1989). We also thank Cathy Grouchy for illustrating the larvae.

Literature cited

Aoki, M., and S. Ueyanagi.
1989. Larval morphology and distribution of the dolphin-fishes, *Coryphaena hippurus* and *C. equiselis* (Coryphaenidae). Tokai Univ. Proc., Oceanogr. Sec., No. 28, p. 157–174. [In Japanese.]

Beardsley, G. L.
1967. Age, growth, and reproduction of the dolphin, *Coryphaena hippurus*, in the straits of Florida. Copeia 1967:441–451.

Berry, F. H., and W. J. Richards.
1973. Characters useful to the study of larval fishes. Mid. Atl. Coast. Fish. Cent. Tech. Pap. 1:48–65.

Briggs, J. C.
1960. Fishes of worldwide (circumtropical) distribution. Copeia 1960(3):171–180.

Collette, B. B., R. H. Gibbs, and G. E. Clipper.
1969. Vertebral numbers and identification of the two species of dolphin (*Coryphaena*). Copeia 1969(3):630–631.

Dawson, C. E.
1971. Occurrence and description of prejuvenile and early juvenile Gulf of Mexico cobia, *Rachycentron canadum*. Copeia (1):65–71.

Ditty, J. G.
1986. Ichthyoplankton in neritic waters of the northern Gulf of Mexico off Louisiana: composition, relative abundance, and seasonality. Fish. Bull. 84: 935–946.

Ditty, J. G., and R. F. Shaw.
1992. Larval development, distribution, and ecology of cobia, *Rachycentron canadum* (Family:

Rachycentridae), in the northern Gulf of Mexico. Fish. Bull. 90:668–677.

Eldridge, P. J., F. H. Berry, and M. C. Miller III.
1977. Test results of the Boothbay neuston net related to net length, diurnal period, and other variables. S. Car. Mar. Resour. Cent. Tech. Rep. No. 18, 22 p.

Fahay, M. P.
1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. NOAA Tech. Rep., NMFS SSRF-685, 39 p.

Gibbs, R. H., Jr., and B. B. Collette.
1959. On the identification, distribution, and biology of the dolphins, *Coryphaena hippurus* and *C. equiselis*. Bull. Mar. Sci. 9(2):117–152.

Govoni, J. J., D. E. Hoss, and D. R. Colby.
1989. The spatial distribution of larval fishes about the Mississippi River plume. Limnol. Oceanogr. 34(1):178–187.

Grimes, C. B., and J. H. Finucane.
1991. Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. Mar. Ecol. Prog. Ser. 75:109–119.

Hassler, W. W., and R. P. Rainville.
1975. Techniques for hatching and rearing dolphin, *Coryphaena hippurus*, through larval and juvenile stages. Univ. N. Carolina Sea Grant Prog., UNC-SG-75–31, 17 p.

Hubbs, C. L., and K. F. Lagler.
1958. The fishes of the Great Lakes region. Univ. Mich. Press, Ann Arbor, 213 p.

Johnson, G. D.
1984. Percoidei: development and relationships, p. 464–498. *In* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson (eds.), Ontogeny and systematics of fishes, p. 464–498. Am. Soc. Ichthy. Herp., Spec. Publ. No. 1.

Kelley, S., T. Potthoff, W. J. Richards, L. Ejsymont, and J. V. Gartner.
1986. SEAMAP 1983—Ichthyoplankton. Larval distribution and abundance of Engraulidae, Carangidae, Clupeidae, Lutjanidae, Serranidae, Sciaenidae, Coryphaenidae, Istiophoridae, Xiphiidae, and Scombridae in the Gulf of Mexico. NOAA Tech. Mem., NMFS-SEFC-167, no pagination.

Lamadrid-Rose, Y., and G. W. Boehlert.
1988. Effects of cold shock on egg, larval, and juvenile stages of tropical fishes: potential impacts of ocean thermal energy conversion. Mar. Environ. Res. 25:175–193.

Leis, J. M., and T. Trnski.
1989. The larvae of Indo-Pacific shorefishes. Univ. Hawaii Press, Honolulu, 371 p.

Mito, S.
1960. Egg development and hatched larvae of the common dolphin-fish *Coryphaena hippurus* Linne. Bull. Jap. Soc. Sci. Fish. 26:223–226.

Okiyama, M.
1988. An atlas of the early stage fishes in Japan. Tokai Univ. Press, Tokyo, p. 481–483.

Palko, B. J., G. L. Beardsley, and W. J. Richards.
1982. Synopsis of the biological data on dolphinfishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. NOAA Tech. Rep., NMFS Circ. 443, 28 p.

Pauly, D., and R. S. V. Pullin.
1988. Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environ. Biol. Fish. 22(4):261–271.

Potthoff, T.
1971. Observations on two species of dolphin (*Coryphaena*) from the tropical mid-Atlantic. Fish. Bull. 69:877–879.

1980. Development and structure of fins and fin supports in dolphin fishes *Coryphaena hippurus* and *Coryphaena equiselis* (Coryphaenidae). Fish. Bull. 78:277–312.

Powles, H.
1981. Distribution and movements of neustonic young of estuarine dependent (*Mugil* spp., *Pomatomus saltatrix*) and estuarine independent (*Coryphaena* spp.) fishes off the southeastern United States. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178:207–209.

Powles, H., and B. W. Stender.
1976. Observations on composition, seasonality and distribution of ichthyoplankton from MARMAP cruises in the South Atlantic Bight in 1973. South Car. Mar. Res. Cent. Tech. Rep. Ser. No. 11, 47 p.

Richardson, S. L., and W. A. Laroche.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (Family Scorpaenidae) off Oregon. Fish. Bull. 77:1–46.

Richards, W. J., T. Potthoff, S. Kelley, M. F. McGowan, L. Ejsymont, J. H. Power, and R. M. Olvera L.
1984. SEAMAP 1982—Ichthyoplankton. Larval distribution and abundance of Engraulidae, Carangidae, Clupeidae, Lutjanidae, Serranidae, Coryphaenidae, Istiophoridae, Xiphiidae, and Scombridae in the Gulf of Mexico. NOAA Tech. Mem., NMFS-SEFC-144, no pagination.

Richards, W. J., T. Leming, M. F. McGowan, J. T. Lamkin, and S. Kelley-Fraga.
1989. Distribution of fish larvae in relation to hydrographic features of the Loop Current boundary in the Gulf of Mexico. Rapp. P. v. Reun. Cons. int. Explor. Mer 191:161–176.

Rose, C. D.
1966. The biology and catch distribution of the dolphin *Coryphaena hippurus* (Linnaeus) in North Carolina waters. Ph.D. diss., N. Carolina State Univ., Raleigh, 153 p.

Sanders, N., Jr., T. Van Devender, and P. A. Thompson.
1990. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1986. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 20, 328 p.

SAS Institute, Inc.
1985. SAS User's Guide: Statistics, 1985 ed. SAS Institute, Cary, NC, 584 p.

Schuck, H. A.
1951. Notes on the dolphin (*Coryphaena hippurus*) in North Carolina waters. Copeia 1951(1): 35–39.

Shcherbachev, Y. N.
1973. The biology and distribution of the dolphins (Pisces, Coryphaenidae). J. Ichthyol. 13:182–191.

Soichi, M.
1978. Spawning behavior of the dolphin, *Coryphaena hippurus*, in the aquarium and its eggs and larvae. Jap. J. Ichthyol. 24:290–294. [In Jap., Engl. summ.]

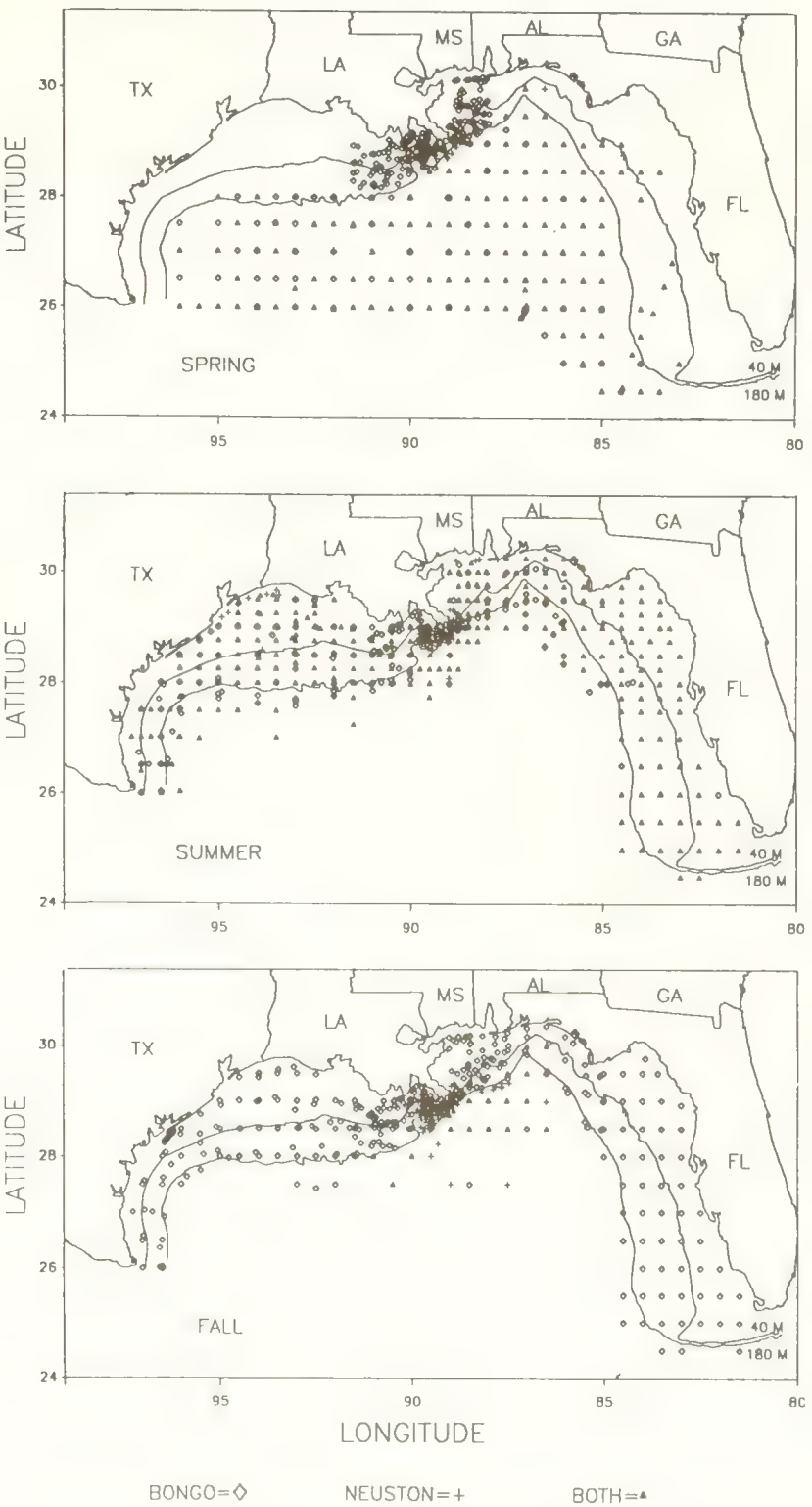
Stuntz, W. E., C. E. Bryan, K. Savastano, R. S. Waller, and P. A. Thompson.
1985. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1982. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 12, 145 p.

Thompson, P. A., and N. Bane.
1986a. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1983. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 13, 179 p.
1986b. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1984. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 15, 171 p.

Thompson, P. A., T. Van Devender, and N. J. Sanders Jr.
1988. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1985. Gulf States Marine Fish. Comm., Ocean Springs, MS, No. 17, 338 p.

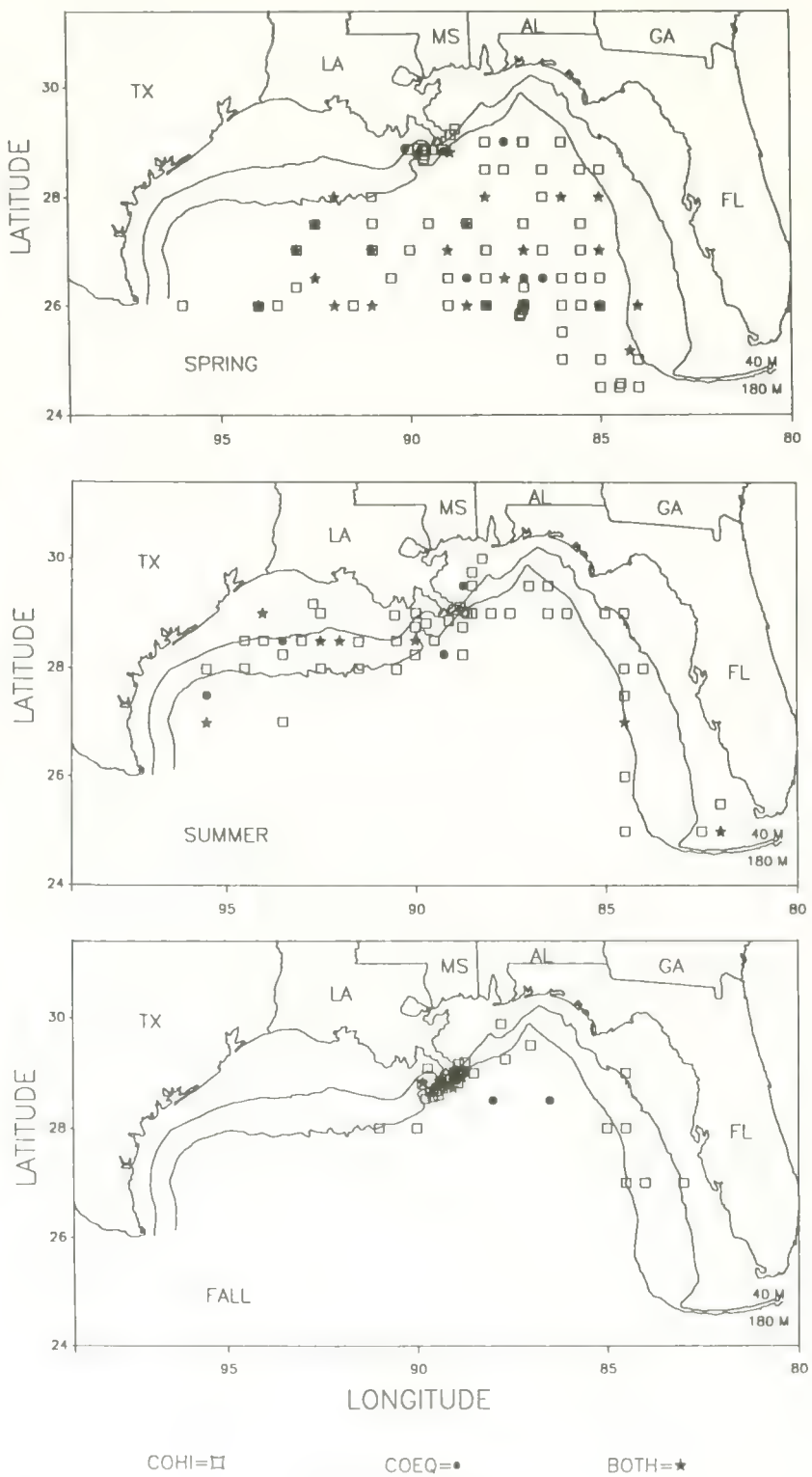
Uchiyama, J. H., R. K. Burch, and S. A. Kraul Jr.
1986. Growth of dolphins, *Coryphaena hippurus* and *C. equiselis*, in Hawaiian waters as determined by daily increment on otoliths. Fish. Bull. 84:186–191.

Zar, J. H.
1984. Biostatistical analysis. Second ed., Prentice-Hall, Inc., NJ, 718 p.



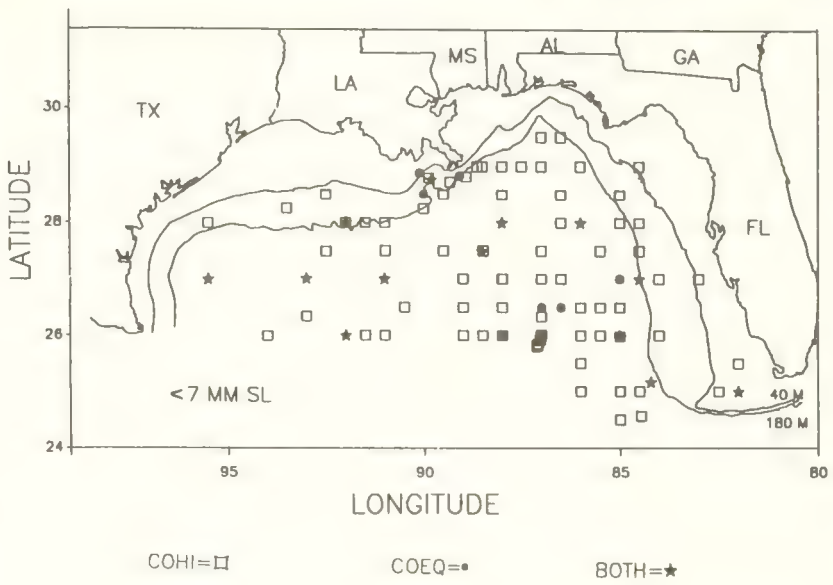
Appendix Figure 1

Distribution of sampling by season for the northern Gulf of Mexico. Seasons are combined across years. Spring (March-May), summer (June-August), fall (September–November).



Appendix Figure 2

Distribution of common dolphin (*Coryphaena hippurus*) and pompano dolphin (*C. equiselis*) larvae in the northern Gulf of Mexico by season. Seasons are combined across years. Catches are from both bongo and neuston net tows. Spring (March–May), summer (June–August), fall (September–November).



Appendix Figure 3

Distribution of early larval (<7.0 mm) common dolphin (*Coryphaena hippurus* [COHI]) and pompano dolphin (*C. equiselis* [COEQ]) in the northern Gulf of Mexico. Both bongo and neuston net tows are used in determining early larval distribution. Data are combined across seasons and years.

Abstract.—Age determination of sablefish (*Anoplopoma fimbria*) is typically done by counting growth zones on the burnt cross-section of the otolith. The break-and-burn method of age determination is difficult to apply to sablefish. Therefore, we applied a relatively new method of fish age validation, using the disequilibrium of Pb-210/Ra-226 in the otoliths. This method of validation complements previous methods which used oxytetracycline (OTC) marking to validate incremental growth in sablefish otoliths. The Pb-210/Ra-226 disequilibria generally confirmed the ageing criteria used to interpret the otolith's burnt cross-section.

Using Pb-210/Ra-226 disequilibria for sablefish, *Anoplopoma fimbria*, age validation

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Sablefish (*Anoplopoma fimbria*) is an important commercial species distributed continuously along the North Pacific Rim from California to northern Japan. On central California's continental shelf, the spawning of sablefish takes place from October to February at depths of over 823 m (Hunter et al., 1989). Both eggs and larvae have been collected at depths of over 400 m in April off British Columbia. After hatching, postlarval sablefish move into the surface waters where onshore or offshore transport may take place (Mason et al., 1983). Postlarvae have been found offshore, but as juveniles they are usually seen inshore (Bracken, 1983; Mason et al., 1983). The juveniles are believed to reside inshore for several years and then move to deeper offshore waters as they near maturity and join the spawning population (Bracken, 1983; Mason et al., 1983). Mature sablefish are typically caught at 700 m (Mason et al., 1983). Funk and Bracken[1] note that the growth of young fish is fast compared to very slow growth of mature fish. An abrupt slowing of growth coincides with the onset of sexual maturity. Mean fork length increases with depth and the length at 50% maturity for females is 60 cm (Hunter et al., 1989).

At the Alaska Fisheries Science Center (AFSC) sablefish ages are determined by counting growth zones (assumed annular) seen on the distal surface of the otolith, or more frequently in the burnt dorsal-ventral cross-section (break-and-burn method, Beamish et al., 1983). Even though ageing criteria have been established for sablefish by using the break-and-burn method (Beamish and Chilton, 1982; Beamish et al., 1983), variability between individual sablefish in the morphology of their otoliths and the appearance of growth zones makes this method difficult to apply. Between-reader variability in sablefish ages are far greater than for any other species routinely aged at the AFSC (Kimura and Lyons, 1991).

Sablefish age validation has been examined by using oxytetracycline (OTC) studies, mark and recapture of known age fish, tagging studies, length-frequency analysis of young fish, and daily growth zone counts in juvenile sablefish otoliths (Beamish

[1] Funk, F., and B. E. Bracken. 1983. Growth of sablefish in southeastern Alaska. AK Dept. Fish and Game Info. Leaflet No. 223, 40 p.

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Fishery Bulletin 92:292-301 (1994)

and Chilton, 1982; Beamish et al., 1983). The age range considered by Beamish and Chilton (1982) was from 0 to 43 years, but their study had few individuals from the upper end of the age range. The OTC method can validate only incremental growth zones after injection, leaving interpretation of earlier growth in any one fish questionable. Ideally, the age range of OTC-injected fish spans all ages. Younger OTC-injected fish can then be used to infer that incremental growth zones seen prior to an OTC injection on older fish are annuli. With these limitations, the procedures used by Beamish and Chilton (1982) and Beamish et al. (1983) confirmed that ages counted on the burnt cross-section were accurate.

Our goal was to use radiometric dating techniques to validate the break-and-burn ageing criteria used at the AFSC for sablefish aged to approximately 35 years. This validation used the measured ratio of Pb-210/Ra-226 in the otoliths to provide estimates of total age, thereby complementing previous OTC validation work which only confirmed incremental growth.

In the first application of radiometric ageing to fishes, Bennett et al. (1982) used the ratio of Pb-210/Ra-226 to validate ages up to 80 years for splitnose rockfish (*Sebastes diploproa*). More recently, these radioisotopes were used by Campana et al. (1990) and Fenton et al. (1990, 1991) in age validation and longevity studies in a variety of fish species. Additional radioisotope pairs such as Th-228/Ra-228 have also been used to age fish (Smith et al., 1991).

The isotopes Ra-226 and Pb-210 are part of the naturally occurring decay chain of U-238:

$$\begin{array}{ccccccc} U\text{-}238 & \dashrightarrow & Ra\text{-}226 & \dashrightarrow & Rn\text{-}222 & \dashrightarrow & Pb\text{-}210 \\ 4.5\times10^{9}\,yr & & 1600\,yr & & 3.8\,d & & \\ Pb\text{-}210 & \dashrightarrow & Po\text{-}210 & \dashrightarrow & Pb\text{-}206 & & \\ 22.3\,yr & & 138\,d & & & & \end{array} \quad (1)$$

where the dashed lines indicate short-lived intermediary nuclides that are not shown.

Both Ra-226 and Pb-210 are found naturally in seawater. Ra-226 is a calcium (Ca) analogue which accompanies Ca through the food chain and is deposited in fish tissue, particularly calcified structures, along with Ca (Swanson, 1985; Porntepkasemsan and Nevissi, 1990). The otoliths of teleosts consist of an acellular organic protein matrix mineralized with aragonite, a form of calcium carbonate in which the radioisotopes are deposited (Mugiya, 1977; Campana and Neilson, 1985). Pb-210 is also accumulated by the biota through the food chain (Shannon et al., 1970; Heyraund and Cherry, 1979). In fish, Pb-210 is preferentially deposited in the bone or liver[2] (Swanson, 1985). Its initial activity in the otolith must be measured (later as R^*) for the application of radiometric ageing.

When Ra-226 is deposited in otoliths, like Ca it remains immobile, and a disequilibrium is created between Ra-226 and all of its progeny. With time, the activity of shorter-lived daughter products like Pb-210 will increase. In the pair of radioisotopes used here, Ra-226 and Pb-210, the difference between their half-lives is great (Eq. 1). Therefore, after about 100 years in a closed system the activity of both Ra-226 and Pb-210 will become equal, establishing a so called "state of secular equilibrium" (Faure, 1986). A chronometer is started when Ra-226 is first deposited in the otolith, and the activity ratio Pb-210/Ra-226 is a function of the time elapsed since deposition.

Radiometric dating applied to fish otoliths relies on three basic assumptions (Faure, 1986; Smith et al., 1991):

1 The otoliths are closed with respect to the loss or gain of any radioisotopes in the decay chain.
2 The initial activity ratio of Pb-210/Ra-226 in the otoliths should be much smaller than one, ideally close to zero, and known or measured.
3 The specific activity [disintegrations per minute per gram (dpm/g)] of the radioisotopes in the material incorporated into the otoliths must be constant.

These assumptions will be considered in detail later in the "Discussion" section. But first, it is important to consider Assumption 3 because it explains why we did not use whole otoliths. Assumption 3 is the most problematic of the three assumptions when applied to whole otoliths because it also requires assuming a mass-growth rate for the otoliths (Smith et al., 1991). Campana et al. (1990) used otolith cores in their application of radiometric dating to fish. When using otolith cores and individual measurements of Ra-226 for each sample being radiometrically aged, Assumption 3 becomes unnecessary. However, if measurements of Ra-226 are averaged over the different samples being radiometrically aged, Assumption 3 requires that the different core samples have the same activity levels. Our study followed the procedures of Campana et al. (1990) and used otoliths cores. But unlike Campana et al. (1990), we used individual Ra-226 measurements for each sample being aged so that Assumption 3 was unnecessary.

[2] Noshkin, V. E., K. M. Wong, R. J. Eagle, T. A. Jokela, and J. A. Brunk. 1988. Radionuclide concentrations in fish and invertebrates from Bikini Atoll. Lawrence Livermore National Laboratory, Livermore, Ca., UCRL-53846, 53 p.

Materials and methods

Otolith collection

Sablefish were collected along the Eastern Pacific Continental Shelf during two research cruises by the AFSC. The first collection was made from the research vessel *Alaska* on 8 August 1986 and contained 61 fish captured at 135 m in Morro Bay, California. The second collection was made from the vessel *American Viking* between 23 September and 31 October 1986 and contained 423 fish captured at depths of 246–1426 m off the California coast between 32°23'N and 42°23'N. Both sagittal otoliths were removed at sea. The sacculus membranes were removed and otoliths were stored in 50% ethanol.

Ages were estimated by the first author (Reader 1) from one otolith per fish applying the break-and-burn method, and the other otolith was used in the radiometric study. The criteria used to count annuli for this study were similar to those typically used by experienced age readers at the AFSC and Tiburon Laboratories of the National Marine Fisheries Service (NMFS), and were the same used by Beamish and Chilton (1982) and Beamish et al. (1983). By using these criteria, an age range of up to ±5 years for older fish was often possible. The oldest age consistent with these criteria was often assigned as the most probable age. When a fish was aged as 1 year old the otolith surface was usually adequate and no break-and-burn was done. The otoliths were subsequently pooled into four age categories (1 year, 9–11 year, 14–23 year, and 24–34 year), on the basis of Reader-1 ages.

For comparison, a subsample of otoliths initially aged ≥14 years (n=186) was read by a second experienced sablefish age reader at the AFSC (Reader 2). Additionally, all fish initially aged ≥14 years (n=266) were read by an experienced sablefish age reader at the Pacific Biological Station (PBS), Canadian Department of Fisheries and Oceans (Reader 3).

In the radiometric dating procedures, we used that part of the otolith which was deposited during the first year of life (i.e. the first year core). For age category 1, whole otoliths representing the first 15 to 18 months of growth were used. These otoliths were those classified as age 1 by Reader 1 and were intact and unburnt. For other age categories, the first year cores were isolated by grinding away excess otolith material. The grinding was done with a Buehler metallurgical polishing machine equipped with Buehler wet and dry #600 or #900 paper. Otolith material representing the first year was readily identifiable in older fish from the distal surface of the ground otolith, and from the broken-and-burnt section, viewed with a dissecting microscope (25×) as a guide. Removal of material was done slowly, with frequent viewing of the otolith during the grinding process (Kastelle, 1991). The position of the first annulus on the otolith has been confirmed by several authors in age validation studies of young sablefish (Beamish and Chilton, 1982; Beamish et al., 1983; McFarlane and Beamish, 1983). Average measurements of the core dimensions were not used as an aid in the grinding process. Instead, grinding was completed when the contours of the first year were approximated. Small inaccuracies in the grinding were inconsequential because samples were pooled into four categories based on age ranges.

All otolith cores were cleaned with an ultrasonic cleaner in distilled and deionized water for a minimum of 30 seconds. Any soft tissue remaining on the otolith after collection was visibly broken down by the ultrasonic cleaner. The goal of the cleaning was to remove any contamination from soft tissue or grinding paper. After cleaning, the otoliths were stored again in a fresh 50% ethanol solution prior to analysis for radioisotopes.

Approximately one gram of material was necessary for radioisotope activity to be measurable above background levels, which meant that 83 to 141 otoliths were used for each age category. To increase the weight of category 1 (1 year olds), an additional unburnt half of the aged otolith from some specimens was included with the intact otoliths (83 specimens total: 83 whole otoliths plus 65 half otoliths from some of the same fish).

Activity measurements

The methods employed in the chemical separation and counting techniques for Ra-226 and Pb-210 were similar to those used by Bennett et al. (1982) and are detailed in Kastelle (1991).

In general, the activity of Pb-210 in the otoliths was determined by counting the alpha decays of Po-210 (the granddaughter-proxy of Pb-210 with which it is in secular equilibrium, Eq. 1) by using a yield tracer of Po-209. Reagent blanks, with and without yield tracers, were processed with each age category as follows: category 1, one blank without yield tracer; categories 2 and 3 processed simultaneously, one blank with a yield tracer and one without; category 4, one blank with a yield tracer and one without. The counting time for each sample or reagent blank was approximately three weeks.

The activity of Ra-226 was determined by counting alpha decays of Rn-222 (the daughter-proxy of Ra-226 with which it grows into secular equilibrium,

Eq. 1) in a Lucas cell (Lucas, 1957). The samples were stored in a Rn-222 de-emanation flask for a minimum of three weeks prior to counting. During storage, Rn-222 reached secular equilibrium with Ra-226. Reagent blanks were processed with each sample. Lucas cell (Rn-222) counting times were 4,000 minutes for each sample or reagent blank. Lucas cell and electronic backgrounds (counting time 1,000 minutes) were measured multiple times before and after any sample or reagent blank. The counting efficiency (i.e. the percentage of decays that was detected) of the de-emanation technique, Lucas cells, and associated electronics was determined to be 53.75% with the use of a Ra-226 standard solution supplied by the U.S. Environmental Protection Agency. Activities of Ra-226 and associated errors were calculated by using the methods of Sarmiento et al. (1976). Details concerning incorporation of blank and background measurements into the activity calculation for Po-210 and Ra-226 are given in Kastelle (1991). All sources of error were propagated through the calculations to estimate errors (standard deviation or SD) for the Ra-226 and Pb-210 measurements.

Data analysis

ANOVA with contrasts was used to test whether break-and-burn otolith ages from the different age readers were significantly different within each age category. Statistical analyses of activity measurements from samples, backgrounds, and reagent blanks were conducted by using Z, t, and a likelihood ratio χ^2 test as described below. To test if the Ra-226 (or Pb-210) activity from each age category was statistically different, the likelihood ratio test was employed. Assuming X_i is distributed as $N(\mu_i,\sigma_i^2)$, where the σ_i^2 are known, the likelihood ratio χ^2 test for $H_o: \mu_1 = ... = \mu_n$, is

$$\hat{\chi}^2 = \sum (X_i - \hat{\mu})^2 / \sigma_i^2$$

which is distributed as χ^2_{n-1}. Here X_i is the measured Ra-226 (or Pb-210) activity for age category i,

$$\hat{\mu} = \sum (X_i / \sigma_i^2) / \sum (1/\sigma_i^2),$$

and σ_i^2 is the variance for age category i. If σ_i^2's are underestimated, then the $\hat{\chi}^2$ would be inflated. Z tests were carried out between the reagent blanks plus background, and background alone, for Po-209 and Po-210 measurements; a t-test was performed between the mean Rn-222 reagent blank plus background and the background alone.

Two sets of estimated Pb-210/Ra-226 ratios were calculated: one by using the mean Ra-226 activity from the four categories and the second by using the Ra-226 activity measured for each category. The delta method was used to determine the variance of the ratios (Seber, 1982).

The measured ratio of Pb-210/Ra-226 in the otoliths can be used to predict a radiometric age from the curve:

$$\frac{A_2}{A_1} = 1 - e^{-\lambda_2 t} + R^* e^{-\lambda_2 t}, \qquad (2)$$

where A_1 is the activity for Ra-226, A_2 and λ_2 are the activity and decay constant respectively (λ=ln (2)/half-life, for Pb-210, t is time (i.e. age), and R^* is the initial ratio of Pb-210/Ra-226 (Fig. 1, see also Kastelle [1991]). The initial ratio was estimated by solving Equation 2 for R^* and applying the activity ratio from age category 1 (R^*=-0.034). The negative value for R^* is due to measurement error. Therefore, we assume $R^* = 0$ in Figure 1. The actual fish ages were predicted from the radiometric ages by subtracting the time between collection and analysis (4.5 yr) from the radiometric ages in Figure 1. Alternatively, it is possible to calculate the radiometric ages by correcting the Pb-210 activity estimates to the time of otolith collection. These adjusted radiometric ages were then compared with ages read from the burnt otolith cross-section by the three readers. For each of the readers, a linear regression line was fit through the origin and compared with the 45° line of agreement by using a t-test.

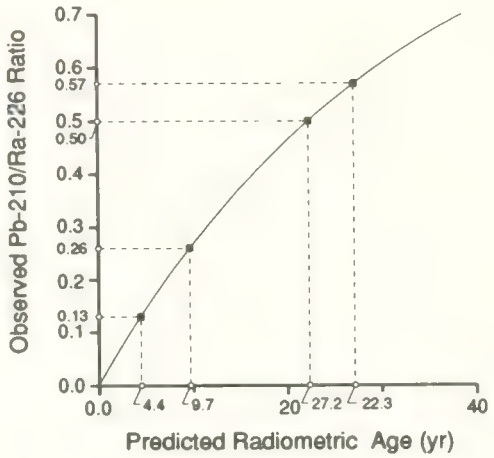

Figure 1

Predicted radiometric age of samples from observed activity ratios and curve of expected activity ratio (Eq. 2). Predicted radiometric age includes the 4.5 years between collection and analysis.

Results

ANOVA with contrasts showed the average age generated by the three age readers within each age category were all pair-wise significantly different ($P<0.001$). Reader 3 estimated the youngest ages, followed by Reader 1, and Reader 2 produced the highest ages (Table 1). Age categories were based on ages from Reader 1; therefore, the age ranges in each category for Readers 2 and 3 were greater.

The reagent blanks plus background for Po-210 and Po-209 did not contain significant activity above the background alone ($P>0.05$). The background activity for Po-209 and Po-210 ranged up to 6.413×10^{-4} $\pm1.472\times10^{-4}$ cpm (counts per minute) and 5.600×10^{-4} $\pm9.75\times10^{-5}$, respectively (Table 2). Therefore, the unadjusted sample data (including background counts) were reduced by the appropriate background only; no adjustment was made for the reagent blank. Specific activity of Pb-210 at the time of separation from Ra-226 ranged from 0.037 ±0.007 dpm/g in category 1 to 0.265 ±0.041 dpm/g in category 4 (Table 3). The Pb-210 activity levels were significantly different among the four age categories ($P<0.001$).

The average background count ($n=66$) for the Rn-222 system was 8.500×10^{-3} $\pm5.27\times10^{-4}$ cpm. The mean reagent blank plus background for Rn-222 was not significantly greater than the background alone ($P=0.077$). Mean Ra-226 activity ($n=4$) was 0.414 ±0.050 dpm/g (Table 3). Ra-226 values from the four age categories were significantly different ($P<0.001$). Therefore, the Ra-226 measurements were specific to each age category.

The adjusted radiometric ages (from category specific Ra-226 measurements) for age categories 1 to 4 respectively were –0.09, 5.21, 17.83, and 22.66 years. Although the adjusted radiometric ages were consistently younger than the burnt cross-section ages from Reader 1, there was general agreement between the two methods (Fig. 2). A t-test between the slope of a line fit through the origin vs. the 45° line did not show a significant difference for any of the age readers ($P>0.05$).

Discussion

Principal findings

The principal result of this study is that the radiometric ages generally confirmed the burnt otolith ageing criteria that are used to age sablefish by U.S. and Canadian age readers. A factor which facilitated this confirmation is that sablefish otoliths apparently accumulate higher levels of radioisotopes than do other fish species that have been previously studied. We found the specific activities of Pb-210 and Ra-226 in sablefish otoliths (Table 3) to be a full order of magnitude greater than values reported in other species (Bennett et al., 1982; Campana et al., 1990; Fenton et al., 1991). These large differences in activity levels may be explained by biological and environmental considerations. Radium-226 is incor-

Table 1

For each age category of sablefish, *Anoplopoma fimbria*, comparison of average estimated age, number of samples read, age range by each age reader, and radiometric age are shown. The time between collection and analysis (4.5 yr) was subtracted from the radiometric age at the time of analysis to make the ages comparable.

Age category	First Reader: average age (yr), n read, range (yr)	Second Reader: average age (yr), n read, range (yr)	Canada (PBS): average age (yr), n read, range (yr)	Radiometric age: average age (yr), n pooled, range (yr)[1]
1	1, n=83, (1)	—	—	–0.09, n=83 (–0.89, 0.74)
2	9.79, n=130, (9, 11)	—	—	5.21, n=130 (3.40, 7.12)
3	18.91, n=141, (14, 23)	22.07, n=101, (14, 42)	15.58, n=139, (8, 27)	17.83, n=141 (13.05, 23.44)
4	28.55, n=127, (24, 34)	31.01, n=85, (17, 49)	23.75, n=127 (11, 48)	22.66, n=127 (16.50, 30.30)

[1] Based on measured Pb-210/Ra-226 ratio and error with individual Ra-226 measurements and Eq. 2.

Table 2

Comparison of background (Bk) and blank (BL) activity reported in the literature for tracer spikes, Po-210 in equilibrium with Pb-210, and Ra-226. NR = not reported

		Tracer spike (Po-209 or Po-208)	Po-210	Ra-226
This study	Bk (cpm)	$1.867 \times 10^{-4} \pm 5.63 \times 10^{-5}$ to $6.413 \times 10^{-4} \pm 1.472 \times 10^{-4}$	$2.353 \times 10^{-4} \pm 6.53 \times 10^{-5}$ to $5.600 \times 10^{-4} \pm 9.75 \times 10^{-5}$	$8.500 \times 10^{-3} \pm 5.27 \times 10^{-4}$
	Bl (dpm)	Not significant	Not significant	Not significant
Bennett et al. (1982)	Bk (cpm)	NR	6.94×10^{-4}	1.4×10^{-2} to 2.8×10^{-2}
	Bl (dpm)	NR	Not measurable above Bk	3.9×10^{-2}
Campana et al. (1990)	Bk (cpm)	NR	6.94×10^{-4}	NR
	Bl (dpm)	NR	5×10^{-4}	NR
Fenton et al. (1990)	Bk (cpm)	NR[1]	NR[1]	
	Bl (dpm)	NR	$1.03 \times 10^{-2} \pm 2.7 \times 10^{-3}$	$1.25 \times 10^{-2} \pm 4.3 \times 10^{-3}$
Fenton et al. (1991)	Bk (cpm)	6.94×10^{-4}	6.94×10^{-4}	1.4×10^{-3} to 3.5×10^{-3}
	Bl (dpm)	NR	$1.03 \times 10^{-2} \pm 2.7 \times 10^{-3}$	$2.55 \times 10^{-2} \pm 2.3 \times 10^{-3}$

[1] Not reported specifically for this radioisotope, but this author suggested a lower value here than reported by Bennett et al. (1982).

Table 3

For each age category of sablefish, *Anoplopoma fimbria*, number of specimens, average estimated age and estimated age range (from Reader 1), specific activity (dpm/gram) of Ra-226 and Pb-210, and the ratios Pb-210/Ra-226 and the ratios Pb-210/mean Ra-226, at the time of analysis 4.5 years after collection are shown. Errors are ±1 SD and are rounded up in the last significant digit for presentation.

Age category	Number pooled	Average age (yr)	Age range (yr)	Ra-226 (dpm/g)	Pb-210 (dpm/g)	Pb-210 Ra-226[1]	Pb-210 Ra-226[2]
1	83	1	1	0.288 ± 0.012	0.037 ± 0.007	0.128 ± 0.023	0.089 ± 0.019
2	130	9.79	9–11	0.517 ± 0.021	0.135 ± 0.022	0.260 ± 0.043	0.325 ± 0.065
3	141	18.91	14–23	0.386 ± 0.017	0.193 ± 0.030	0.500 ± 0.080	0.467 ± 0.092
4	127	28.55	24–34	0.465 ± 0.019	0.265 ± 0.041	0.570 ± 0.091	0.640 ± 0.126

[1] Activity ratios calculated with Ra-226 measured from each group.
[2] Activity ratios calculated with mean Ra-226: 0.414 ± 0.050.

porated into the biota or food chain through a variety of sources, such as water during the osmoregulation process, from food (Porntepkasemsan and Nevissi, 1990) such as phytoplankton (Shannon and Cherry, 1971) and zooplankton (Evans et al., 1938), and from contact with sediments (Swanson, 1985). The geographic area the species inhabits, its vertical distribution in the water column, and the efficiency of transfer of Ra-226 through its food chain could play a role in the uptake of Ra-226 (Cochran,

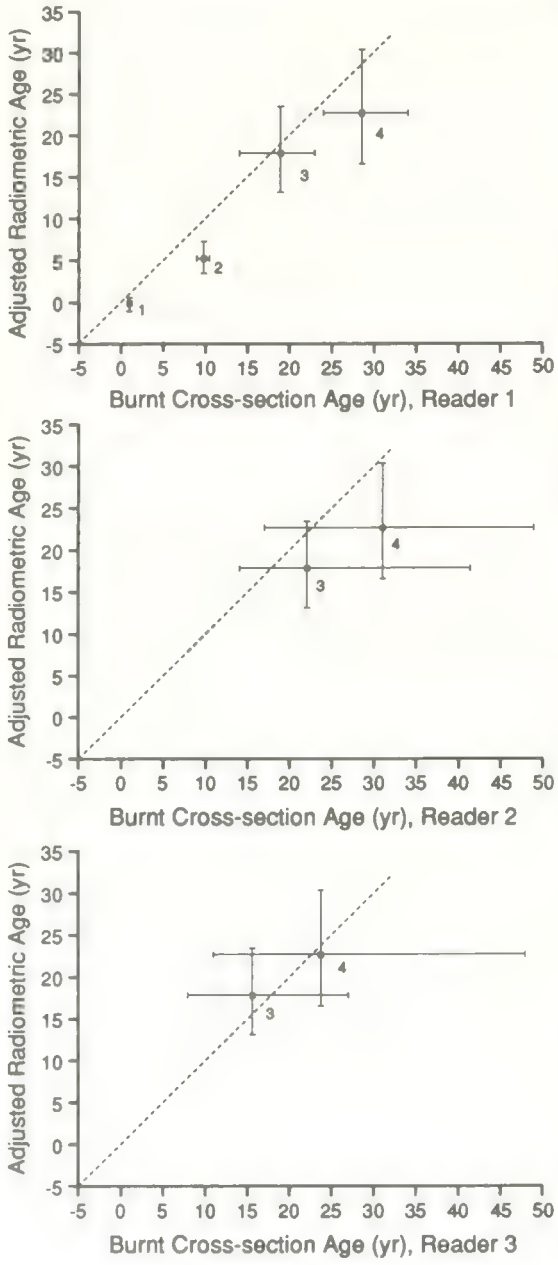

Figure 2

Comparison of burnt otolith cross-section ages (from Readers 1, 2, and 3) with adjusted radiometric ages (4.5 years were subtracted for the time between capture and analysis). Range in adjusted radiometric ages is 1 standard deviation, and the range in burnt otolith cross-section ages are the maximum and minimum in each age category (see Table 1). Ranges of burnt cross-section ages for Readers 2 and 3 are wider than for Reader 1 because age categories were defined by Reader 1 ages.

1982; Swanson, 1985; Fenton et al., 1990). Additionally, feeding rate, metabolic rate, and calcium deposition rate could all affect the specific activities found in otoliths. Sablefish are one of the fastest-growing epipelagic juvenile fishes (Shenker and Olla, 1986; Kendall and Matarese, 1987). Therefore, the higher Ra-226 and Pb-210 activity levels seen in sablefish otolith cores could be related to rapid uptake of Ra-226.

Assumptions for radiometric dating

We discussed three assumptions which must be satisfied for the radioisotope ageing of sablefish to be valid. Assumption 1, that otolith cores are closed with respect to loss or gain of any radioisotopes in the decay chain, has not been tested. Considering the decay chain containing Ra-226 (Eq. 1), Rn-222 is a source of concern. For Ra-226 to decay to Pb-210, it must first become Rn-222 (half-life=3.82 days) which is a noble gas. It is conceivable that Rn-222 could migrate in the otolith. A loss of Rn-222 would lead to underestimation of the true age. However, the calcium carbonate crystalline structure of the otolith probably prevents radioisotopes from migrating.[3]

Welden (1984) measured Pb-210 activity in the calcified cartilage of vertebral centrum from sharks, applying a procedure similar to the dating of sediments. The calcified cartilage allowed the Pb-210 to migrate in the vertebra so the assumption of a closed system did not hold true. Previous research by Goreau and Goreau (1960), Moore et al. (1973), Dodge and Thomson (1974), and Veeh and Burnett (1982) confirmed that calcium carbonate in coral acted as a chemically closed system. In Rn-222 diffusion experiments, Moore et al. (1973) could not detect migrations in coral.

For our study, Assumption 2 required that in the core of otoliths, initial ratios of the two radioisotopes be measured or known, and ideally be near zero. More Ra-226 than Pb-210 may be encountered by fish since Ra-226 is not in equilibrium with Pb-210 in seawater (Bacon et al., 1976). The environmental residence time of Ra-226 in seawater has been reported to be as high as 950 years (Szabo, 1967) and as low as 0.7 to 5.5 years (Shannon and Cherry, 1971). The environmental residence time of Pb-210 in surface waters has been reported to be as high

[3] At the "CSIRO, International workshop on otolith chemistry" 2–6 March 1992, in Hobart, Tasmania, Australia the possibility of Rn-222 migration was discussed with some enthusiasm. G. Fenton suggested that the otolith is relatively impermeable, and that Rn-222 migration is not a major problem

as 3.5 years (Shannon et al., 1970) and as low as 1.4 years (Bacon et al., 1976). Pb-210 is incorporated into particulate matter whereby it is removed from the water column and deposited into sediments. To correct for Pb-210 incorporation, we measured the initial ratio, R^*, with young fish (1 yr olds). By analyzing very young splitnose rockfish, Bennett et al. (1982) found that the initial ratio of Pb-210/Ra-226 was between 0.1 and 0.2. Similar values for the initial ratio were also found in redfish (*Sebastes mentella*) (Campana et al., 1990), orange roughy (*Hoplostethus atlanticus*) (Fenton et al., 1991), and blue grenadier (*Macruronus novaezelandiae*) (Fenton et al., 1990). These results are comparable with the $R^*=0$ we used. The initial ratio cannot be estimated from older age categories because their true ages are uncertain. Therefore, $R^*=0$ for older age categories was assumed.

Assumption 3 states that the specific activity of Ra-226 incorporated into the otolith core be constant over the time span that the otoliths are receiving the radioisotopes. Assumption 3 is not required if only the otolith core is used and individual Ra-226 measurements are made for each age category. In sablefish the core of 1–year-old fish was appropriate because it is large, and there is a strong possibility that fish migration prior to maturity might cause a change in Ra-226 uptake. The likelihood ratio χ^2 test suggested that Ra-226 measurements differed among age categories. Therefore, ratios calculated by using individual Ra-226 measurements were preferred over those calculated with the Ra-226 mean. Campana et al. (1990), using cores composed of the first 5 years of growth, and a mean of 5 whole otolith samples (13 g per sample), found no significant difference in Ra-226 activity between the cores and whole otoliths. This suggested a constant rate of Ra-226 uptake. The differences we found between the Ra-226 activity measured in the four age categories were considerable (Table 3). Because the factors controlling Ra-226 uptake are complex and not well understood, the observed differences may well be real.

The use of whole otoliths requires modeling the mass growth rate of the otolith over the life of the fish and making assumptions concerning the uptake of Ra-226 and Pb-210 each year. Bennett et al. (1982) modeled the otolith's mass growth rate and assumed that the uptake of Ra-226 over the life span of the fish was proportional to otolith size (i.e. they assumed a constant rate of uptake). In whole otoliths from blue grenadier, the rate of uptake of Ra-226 changed over the life of the fish (Fenton et al., 1990). Therefore, the assumption of a constant rate of uptake of Ra-226 was violated. In whole otoliths from orange roughy, the Ra-226 specific activity increased with age (Fenton et al., 1991). Therefore, Fenton et al. (1991) used two Ra-226 averages: one for young age categories and a second for old age categories.

The conservative approach is to use the otolith core and individual category Ra-226 measurements making Assumption 3 unnecessary. Also, by using cores the closed system considered under Assumptions 1 and 2 is reduced. The behavior of otolith material deposited later in a fish's life need not be considered. The different approaches (otolith core, whole otolith, larger multi-gram samples, or any averaging of different age ranges) have trade-offs which should be evaluated in light of a species' biology.

Sources of error in ageing methodologies

Differences between the three sets of burnt cross-section ages are explainable. First, storage of broken-and-burnt otoliths in ethanol between readings may cause a fading of growth patterns. Second, variations in application of the otolith interpretation criteria of Beamish and Chilton (1982) and Beamish et al. (1983) could also lead to differences.

Even with the high specific activity (compared with other species) found in sablefish otoliths, the generally low activity levels of Po-210 and Ra-226 found in otoliths makes it important to carefully evaluate reagent blanks and background activities. Therefore, activity levels for reagent blank and background measurements reported in four previous studies (Bennett et al., 1982; Campana et al., 1990; and Fenton et al., 1990, 1991) were compared with those found here (Table 2). Considering the magnitude of errors, the Po-210 background we found was similar to other reported values (Table 2). The literature showed a much greater range of activities measured in the reagent blanks. Like Bennett et al. (1982), we found a nonsignificant activity level in the Po-210 reagent blank. The Po-210 reagent blank of 0.0103 ±0.0027 dpm reported by Fenton et al. (1990, 1991) seems high compared with the other findings. Also, we were the only study to report a nonsignificant Ra-226 reagent blank activity. Except for the Ra-226 reagent blank result, our background and reagent blank measurements for both Ra-226 and Pb-210 are in the same range as those reported in previous applications of radiometric ageing to fish.

The Ra-226 (or equivalent Rn-222) activity levels were low and difficult to measure. The signal to background ratio can be increased by using a greater sample weight. Fenton et al. (1991) argued that measuring Ra-226 by using barium co-precipitation with alpha spectroscopy (Sill, 1987) could also produce a better signal to background ratio. How-

ever, our measurements of Ra-226 background were similar to those of Fenton et al. (1991).

The low activity of Ra-226 and Pb-210 in the otoliths also requires that care be taken to avoid contamination. The otoliths were stored in 50% ethanol at sea. The grade of the ethanol was not ultra-pure which could introduce contaminating radioisotopes. Ethanol may also leach out some of the radioisotopes during storage. Some previous fish age-validation studies using Pb-210/Ra-226 (Fenton et al., 1990) stored the otoliths dry with desiccated adhering tissues. The dry tissue proved very difficult to remove and introduced Po-210 contamination. We relied on ultrasonic cleaning to break up any soft hydrated tissue after which the otoliths were rinsed thoroughly. This appeared to remove any organic material on the surface of the otolith. Contamination by Po-210 in the adherent tissues would increase the estimated radiometric age. In our study, the results from age category 1 indicate that this was not the case. Also, the grinding paper used could also introduce contamination.

Conclusions

The goal of this study was to validate the break-and-burn otolith ageing criteria used for sablefish at the AFSC. Although usually lower, the radiometric ages were within two standard deviations of the break-and-burn ages (Table 1; Fig. 2). If a range of possible ages occurred in the break-and-burn method, the older age was usually chosen. Since radiometric ages were consistently lower than burnt cross-section ages (from Reader 1), this method was probably not the best way to interpret the broken-and-burnt otolith. Possible migration of Rn-222 from the otolith, as discussed earlier, could also explain the difference.

Nevertheless, the break-and-burn method of age determination for sablefish has been validated by this study for fish up to 34 years old. This is the maximum age regularly seen in commercial or research catches. We have shown that the break-and-burn ageing criteria applied to sablefish otoliths produces, on average, ages similar to radiometric ages.

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Literature cited

Bacon, M. P., D. W. Spencer, and P. G. Brewer.
1976. $^{210}Pb/^{226}Ra$ and $^{210}Po/^{210}Pb$ disequilibria in seawater and suspended particulate matter. Earth Planet. Sci. Lett. 32:277–296.

Beamish, R. J., and D. E. Chilton.
1982. Preliminary evaluation of a method to determine the age of sablefish (*Anoplopoma fimbria*). Can. J. Fish. Aquat. Sci. 39:277–287.

Beamish, R. J., G. A. McFarlane, and D. E. Chilton.
1983. Use of oxytetracycline and other methods to validate a method of age determination for sablefish. *In* Proceedings of the second Lowell Wakefield fisheries symposium, Anchorage, AK, p. 95–116. Alaska Sea Grant Report 83-8.

Bennett, J. T., G. W. Boehlert, and K. K. Turekian.
1982. Confirmation of longevity in (*Sebastes diploproa*) (Pisces: Scorpaenidae) from $^{210}Pb/^{226}Ra$ measurements in otoliths. Mar. Bio. 71:209–215.

Bracken, B. E.
1983. Sablefish migration in the Gulf of Alaska based on tag recoveries. *In* Proceedings of the second Lowell Wakefield fisheries symposium, Anchorage, AK, p. 185–190. Alaska Sea Grant Report 83–8.

Campana, S. E., and J. D. Neilson.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014–1032.

Campana, S. E., K. C. T. Zwanenburg, and J. N. Smith.
1990. $^{210}Pb/^{226}Ra$ determination of longevity in redfish. Can. J. Fish. Aquat. Sci. 47:163–165.

Cochran, J. K.
1982. The oceanic chemistry of the U- and Th-series nuclides. *In* M. Ivanovich and R. S. Harmon (eds.), Uranium series disequilibrium: applications to environmental problems, p. 384–430. Oxford Univ. Press, NY.

Dodge, R. E., and J. Thomson.
1974. The natural radiochemical and growth records in contemporary hermatypic corals from the Atlantic and Caribbean. Earth Planet. Sci. Lett. 23:313–322.

Evans, R. D., A. F. Kip, and E. G. Moberg.
1938. The radium and radon content of Pacific Ocean water, life, and sediments. Am. J. Sci. 36:241–259.

Faure, G.
1986. Principles of isotope geology. John Wiley and Sons, New York, NY, 589 p.

Fenton, G. E., D. A. Ritz, and S. A. Short.
1990. $^{210}Pb/^{226}Ra$ disequilibria in otoliths of blue grenadier, *Macruronus novaezelandiae*: problems associated with radiometric ageing. Aust. J. Mar. Freshwater Res. 41:467–473.

Fenton, G. E., S. A. Short., and D. A. Ritz.
1991. Age determination of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae)

using ^{210}Pb:^{226}Ra disequilibria. Mar. Bio. 109:197–202.

Goreau, T. F., and N. I. Goreau.
1960. The physiology of skeleton formation in corals. IV: On isotopic equilibrium exchanges of calcium between corallum and environment in living and dead reef-building corals. Biol. Bull. Mar. Biol. Lab., Woods Hole 119:416–427.

Heyraund, M., and R. D. Cherry.
1979. Polonium-210 and lead-210 in marine food chains. Mar. Biol. 52:227–236.

Hunter, J. R., B. J. Macewicz, and C. A. Kimbrell.
1989. Fecundity and other aspects of the reproduction of sablefish (*Anoplopoma fimbria*) in central California waters. CalCOFI Rep. 30:61–72.

Kastelle, C. R.
1991. Radioisotope age validation and an estimate of natural mortality from the gonad to somatic weight index for sablefish (*Anoplopoma fimbria*). M.S. thesis, Univ. Washington, School of Fisheries, 87 p.

Kendall, A. W., and A. C. Matarese.
1987. Biology of eggs, larvae, and epipelagic juveniles of sablefish (*Anoplopoma fimbria*) in relation to their potential use in management. Mar. Fish. Rev. 49(1):1–13.

Kimura, D. K., and J. J. Lyons.
1991. Between-reader bias and variability in the age-determination process. Fish. Bull. 89:53–60.

Lucas, H. F.
1957. Improved low-level alpha scintillation counter for radon. Rev. Sci. Instruments 28(9): 680–683.

McFarlane, G. A., and R. J. Beamish.
1983. Preliminary observations on the juvenile biology of sablefish (*Anoplopoma fimbria*) in waters off the west coast of Canada. *In* Proceedings of the second Lowell Wakefield fisheries symposium, Anchorage, AK, p. 119–135. Alaska Sea Grant Report 83–8.

Mason, J. C., R. J. Beamish, and G. A. McFarlane.
1983. Sexual maturity, fecundity, spawning, and early life history of sablefish (*Anoplopoma fimbria*) off the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 40:2126–2134.

Moore, W. S., S. Krishnaswami, and S. G. Bhat.
1973. Radiometric determinations of coral growth rates. Bull. Mar. Sci. 23(2):157–176.

Mugiya, Y.
1977. Effect of acetazolamide on the otolith growth of goldfish. Bull. Jpn. Soc. Sci. Fish. 43(9):1053–1058.

Porntepkasemsan, B., and A. E. Nevissi.
1990. Mechanism of radium-226 transfer from sediments and water to marine fishes. Geochem. J. 24:223–228.

Sarmiento, J. L., D. E. Hammond, and W. S. Broecker.
1976. The calculation of the statistical counting error for ^{222}Rn scintillation counting. Earth Planet. Sci. Lett. 32: 351–356.

Seber, G. A. F.
1982. The estimation of animal abundance and related parameters. Macmillan, New York, NY, 654 p.

Shannon, L. V., and R. D. Cherry.
1971. Radium-226 in marine phytoplankton. Earth Planet. Sci. Lett. 11:339–343.

Shannon, L. V., R. D. Cherry, and M. J. Orren.
1970. Polonium-210 and lead-210 in the marine environment. Geochim. Cosmochim. Acta 34:701–711.

Shenker, J. M., and B. L. Olla.
1986. Laboratory feeding and growth of juvenile sablefish, *Anoplopoma fimbria*. Can. J. Fish. Aquat. Sci. 43:930–937.

Sill, C. W.
1987. Determination of Radium-226 in ores, nuclear wastes and environmental samples by high-resolution alpha spectrometry. Nucl. Chem. Waste Management 7:239–256.

Smith, J. M., R. Nelson, and S. E. Campana.
1991. The use of Pb-210/Ra-226 and Th-228/Ra-228 dis-equilibria in the ageing of otoliths of marine fish. *In* P. J. Kershaw and D. S. Woodhead (eds.), Radionuclides in the study of marine processes, p 350–359. Elsevier Applied Science, England.

Swanson, S. M.
1985. Food-chain transfer of U-series radionuclides in a northern Saskatchewan aquatic system. Health Phys. 49(5):747–770.

Szabo, B. J.
1967. Radium content in plankton and sea water in the Bahamas. Geochim. Cosmochim. Acta 31:1321–1331.

Veeh, H. H., and W. C. Burnett.
1982. Carbonate and phosphate sediments. *In* M.Ivanovich and R. S. Harmon (eds.), Uranium series disequilibrium: applications to environmental problems, p. 459–480. Oxford Univ. Press, NY.

Welden, B. A.
1984. Radiometric verification of age determination in elasmobranch fishes. M.S. thesis, Calif. State Univ., Hayward, Moss Landing Marine Labs, 108 p.

Distribution and abundance of two juvenile tropical *Photololigo* species (Cephalopoda: Loliginidae) in the central Great Barrier Reef Lagoon

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Abstract.—This study quantified the temporal and spatial abundance of juveniles of two *Photololigo* species on the continental shelf off Townsville, Australia with the use of light-traps. The two *Photololigo* species (A and B) showed very distinct and separate spatial distribution patterns. *Photololigo* sp. A was found close to the coast and was the smaller and more abundant of the two species. This species was most abundant in surface waters, although larger individuals were generally caught deeper. There was no evidence of vertical movements during the night. The presence of small and large juvenile *Photololigo* sp. A during summer and winter months suggests spawning and recruitment occur throughout the year. In contrast, *Photololigo* sp. B was caught predominantly offshore. All sizes of *Photololigo* sp. B were caught both near the benthos and at the surface in the mid-lagoon, but farther offshore juveniles were deeper and larger. The presence of small juvenile squid of both species throughout the summer suggests that these species spawn for an extended period during the summer. This study demonstrates that light-traps are an effective way of sampling small cephalopods.

The current poor state of knowledge about processes important in squid population dynamics is mainly due to limited information about the juvenile phase (Voss, 1983; Boyle, 1990). Life-history characteristics have largely been derived from information about the adult phase. Our limited information about young squid is demonstrated in attempting to define the life-history phases (Young and Harman, 1988). Jackson and Choat (1992) suggest, given the comparatively short life time of tropical squid (<250 days), that a proportionally long period of the life cycle is spent as small individuals. In the case of *Loligo chinensis,* with a summer life time of 120 days, individuals less than 60 days old (<50-mm mantle length) have not been studied. Hence, for almost half the life history of most squid there is not even the most basic information. Temporal and spatial abundance patterns of juvenile squid will provide a basis for understanding the processes of mortality, growth, and recruitment. However, such information has traditionally been difficult to obtain because of problems in capturing and identifying a sufficient size range of juvenile cephalopods (Vecchione, 1987).

To examine the ecology of juvenile squid it is necessary to use techniques that catch a size range of individuals, hatchlings to juveniles, in good condition. Pelagic squid produce either benthic or pelagic eggs and have a planktonic juvenile phase (Boletzky, 1977). Juvenile squid are alert, mobile organisms that easily avoid capture by towed nets (Vecchione, 1987). The use of a combination of different towed nets to sample an area enables the collection of a wider size range of juvenile squid (Rodhouse et al., 1992). However, it is difficult to obtain replicates needed to provide density estimates from towed nets. In this study we have employed an alternative technique based on light-attraction that is effective in sampling pelagic juvenile fishes. Automated light-traps (Doherty, 1987) can overcome the problems of net avoidance and enable sampling at discrete depths in the water column. The ability to sample concurrently within an area ensures that estimates of variability in abundance are not confounded by time. This technique also collects live material in good condition, which can facilitate taxonomic identification. However, sampling an unknown volume of

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water by individual traps requires cautious interpretation of abundance estimates (Choat et al., 1993).

There are four species of loliginid squid currently recognized in the Townsville region: *Sepioteuthis lessoniana, Loliolus noctiluca*, *Photololigo* sp. B, and *Photololigo* sp. A.[1] There are currently no morphological descriptions of the two *Photololigo* species, but they can be readily identified by using allozyme electrophoretic techniques (Yeatman and Benzie, in press). Previously both of these species have been referred to as *Photololigo* (*Loligo*) *chinensis* (Jackson and Choat, 1992; Yeatman and Benzie, in press), but neither correspond to *P. chinensis* from Thailand.[2] Electrophoretic analysis of a subset of juveniles collected during three months of the program found that all *Photololigo* sp. A were found less than 33 km offshore and 90% of the *Photololigo* sp. B were found 33 km or more offshore.[2] Because these species are morphologically identical as juveniles, we assumed that all individuals found at stations less than 33 km offshore were *Photololigo* sp. A and that *Photololigo* collected more than 33 km offshore were *Photololigo* sp. B. *Photololigo* sp. A (previously known as *Loligo chinensis*) has been the topic of recent growth studies using statolith aging techniques (Jackson and Choat, 1992). This species is a small short-lived neritic squid. Individuals are approximately 60 days old when they appear in the adult population and they can grow to 180 mm in 120 days. Little is known about the early life-history and juvenile distribution patterns of either *Photololigo* species. The objectives of this study were to describe the spatial and temporal distribution patterns of juvenile *Photololigo* species across the continental shelf in the Townsville region of the Great Barrier Reef.

Materials and methods

Sampling design

Two major habitat types are found on the continental shelf, off Townsville, Australia. The inshore habitat is a 56 km wide soft bottom coastal lagoon ranging in depth from 15 m to 40 m. The offshore habitat is a complex reef matrix of similar extent, dissected by channels ranging from 40 m to 75 m deep at the shelf break. To assess the cross-shelf distribution of juvenile squid, four automated light-traps (Doherty, 1987) were deployed at fifteen sampling stations spanning the continental shelf and the western Coral Sea (Fig. 1). Abundance along this transect was assessed over four months, October to January, during two austral summers, 1990/91 and 1991/92. At each station, the abundance of juvenile squid was determined at two depths by deploying two pairs of light-traps. In each pair, one light-trap was suspended immediately below the surface while the other light-trap was set deeper. In 1990/91, all deep light-traps were suspended 20 m below the surface. In 1991/92, the deep light-traps were suspended within 5 m of the bottom to a maximum of 100 m in the Coral Sea.

In all deployments, the two pairs of light-traps were released approximately 300 m apart and allowed to drift for one hour. Allowing the traps to drift in the water minimized potential problems with differential water movement among stations. The use of drifting light-traps has been shown to be a more effective way of catching pelagic organisms than anchored light-traps in open water (Thorrold, 1992). After one hour, the four light-traps were retrieved and the entire catch was fixed and preserved in 100% ethanol. Each evening the first light-trap was deployed after 1930 hours (Eastern Standard Time) and the last light-trap retrieved before 0430 hours. Travel time between each station allowed only five cross-shelf stations to be sampled per night. Thus, each night's activity concentrated on one of the two continental shelf habitats or the Coral Sea. Each monthly cruise consisted of nine nights during which time each of the 15 stations was sampled three times. However, sea conditions were not always favorable. Sampling effort at each station is shown in Table 1.

It was not logistically possible to sample all stations in each habitat simultaneously. Therefore, time of night is confounded with station position. Haphazard selection of the first station sampled each night ensured that no station was consistently sampled at the same time on all nights. Cruises were scheduled to include the new moon because this is the lunar phase when light attraction has proved most effective for fishes and various invertebrates (Milicich, 1992). Temperature and salinity profiles of the water column were collected at each station by using a Seabird Conductivity Temperature Device during the 1991/92 summer.

Concurrent with the summer cross-shelf sampling, light-traps were anchored within 100 m of the southeasterly side (weather-side) of four reefs; Keeper, Helix, Faraday, and Myrmidon, to sample near-reef water (Fig. 1). The use of drifting light-traps near the reefs was not possible. During the summer of 1990/91, four light-traps were anchored at each reef; three immediately below the surface

[1] C. C. Lu, Museum of Victoria, Australia, pers. commun. 1990.
[2] J. Yeatman, James Cook Univ., Australia, unpubl. data 1993.

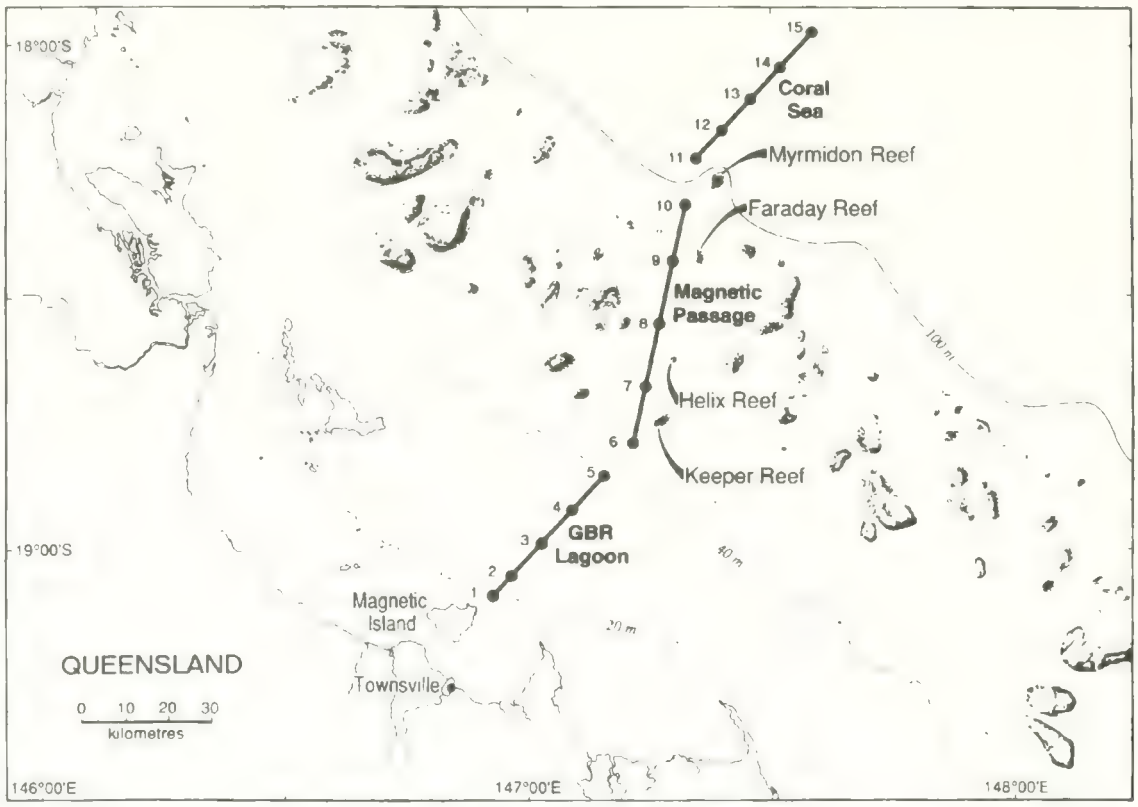

Figure 1

Map of the cross-shelf transect off Townsville, Australia, showing the position of each station along the transect. Station 1 = 19 km from Townsville, 2 = 24 km, 3 = 33 km, 4 = 43 km, 5 = 52 km, 6 = 61 km, 7 = 75 km, 8 = 92 km, 9 = 100 km, 10 = 115 km, 11 = 136 km, 12 = 145 km, 13 = 152 km, 14 = 163 km, and 15 = 172 km.

and one at 20 m below the surface. In 1991/92, an extra light-trap was added at 20 m. The anchored light-traps had an automatic timer, enabling the lights to be switched on and off automatically at predetermined periods during the night. Each light-trap on the reef fished for a total of three hours per night; lights came on for one hour at 2200 hours, 2400, and 0300 hours. Light-traps at all reefs were emptied the following day.

Squid were identified in the laboratory and the dorsal mantle length recorded for each individual. Individuals were measured within 14 days of preservation in 100% ethanol. A comparison of measurements of individuals (ranging in size from 5.3 mm to 29.5 mm) before and 14 days after preservation found that shrinkage was on average 0.5 mm.

Abundance patterns of the two *Photololigo* species during the two summers of sampling were examined by using 'planned comparisons,' where specific pregenerated hypotheses were examined (Day and Quinn, 1989). For each species we were interested in differences in abundance between years, locations, and depths.

To examine seasonality of juvenile *Photololigo* sp. A, the inshore station (19 km) was sampled during the austral winter months of May, June, July, and August 1991. Three sites at this station were sampled with four shallow and four deep (13-m) light-traps. Sites were sampled during the period of the new moon, on five nights in May and three nights in June, July, and August. Densities in summer and winter months were compared by using an unbalanced one-way analysis of variance (ANOVA), with month as the factor analyzed. Values in each light-trap for nights and sites within a month were treated as replicates.

To determine whether vertical migration might influence horizontal distribution patterns we examined the size structure of *Photololigo* sp. A at two depths during the night. On at least one occasion

Table 1

Total sampling effort for *Photololigo* spp. in each month in light-trap hours (and number of nights sampled) at each station during the two summers of sampling.

Year and month	Distance (km) from Townsville														Total no. sampled
	19	24	33	43	52	61	75	92	100	115	136	145	152	163	172	
1990																
Oct	8(2)	15(4)	16(4)	12(3)	16(4)	15(4)	4(1)	4(1)	4(1)	4(1)	12(3)	10(3)	10(3)	10(3)	10(3)	150(40)
Nov	12(3)	12(3)	12(3)	0(0)	16(3)	12(3)	12(3)	12(3)	12(3)	12(3)	8(2)	8(2)	8(2)	4(1)	4(1)	144(35)
Dec	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	3(1)	4(1)	4(1)	4(1)	4(1)	4(1)	4(1)	4(1)	67(17)
1991																
Jan	12(3)	12(3)	12(2)	12(2)	12(2)	8(2)	8(2)	8(2)	8(2)	8(2)	8(2)	8(2)	4(2)	8(2)	8(2)	136(32)
Oct	12(3)	12(3)	12(3)	12(3)	12(3)	12(3)	8(2)	8(2)	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	124(31)
Nov	12(3)	12(3)	11(3)	12(3)	12(3)	12(3)	12(3)	12(3)	12(3)	12(3)	4(1)	4(1)	4(1)	4(1)	4(1)	139(35)
Dec	12(3)	10(3)	11(3)	12(3)	12(3)	12(3)	8(2)	8(2)	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	121(31)
1992																
Jan	12(3)	12(3)	12(3)	11(3)	12(3)	12(3)	8(2)	8(2)	8(2)	8(2)	4(1)	4(1)	4(1)	4(1)	4(1)	123(31)
Total	88(22)	93(24)	90(22)	75(18)	96(22)	87(22)	64(16)	63(16)	64(16)	64(16)	48(12)	46(12)	42(12)	42(11)	42(11)	1004(254)

in each month of the 1991/92 sampling period the 19- and 24-km stations were sampled both early and late in the night. The samples were separated into early (captured before 2400 hrs) and late (captured after 2400 hrs). By combining data from stations, across nights and months, it was possible to compare the size distributions between depths and time of night. A multiway-frequency analysis was used to determine the effect of time of night and depth on the size-frequency distribution.

Results

Distribution patterns

Juvenile *Photololigo* individuals were predominantly caught within 52 km of the mainland (Fig. 2). The few individuals found farther offshore were in the Magnetic Passage (five individuals) and on the reefs (six individuals). *Photololigo* species were not found in the Coral Sea. *Photololigo* sp. A was numerically the most abundant of the two species during both summers (Fig. 2); 856 individuals were caught in 181 hours of light-trapping (4.73 individuals caught per hour), compared with 379 *Photololigo* sp. B caught in 348 hours of light-trapping (1.09 individuals per hour). Catch per hour of light-trapping was greatest for *Photololigo* sp. A, especially at the 24-km station. The catch per unit of effort for *Photololigo* sp. B was greater at the 33-km station (Table 2). Overall, *Photololigo* sp. A juveniles were present in higher numbers at the 24-km station in the surface waters (Table 3). This pattern was consistent in both years, but higher numbers were caught in 1991/92 (Table 3), largely because of very high catches in December 1991 (Fig. 2). In comparison, highest numbers of *Photololigo* sp. B were consistently found at the 33-km station and abundance levels tended to decrease farther offshore (Fig. 2). Overall, *Photololigo* sp. B demonstrated no difference in abundance levels between the two years (Table 4). In contrast to *Photololigo* sp. A, juvenile *Photololigo* sp. B was more abundant deeper in the water column (Table 4). Farther offshore, *Photololigo* sp. B juveniles were present in very low numbers and were caught only in the deep light-traps (Fig. 2).

Photololigo sp. A ranged in size from 2.6 to 47.9 mm. The size-frequency distributions at the two depths were not significantly different between the 19-km and 24-km stations (χ^2=12.28; df=9; P=0.1979) (Fig. 3). There was no systematic change in the size-frequency distribution of *Photololigo* sp. A during either summer (Fig. 4). A modal shift in the size-frequency distribution in January 1992 suggested that fewer small individuals were available to be caught. However, catches were very low in this month.

Photololigo sp. B ranged in size from 3.6 to 61.6 mm (Fig. 3). From the size-frequency distributions it was clear that larger juveniles were found farther offshore and deeper in the water column (Fig. 3). No

modal shift in the size-frequency distribution during the summers was apparent (Fig. 4). However, catches were low in most months.

The multiway-frequency analysis established that the size-frequency distribution of juvenile *Photololigo* sp. A at both depths changed as a function of time of night (Table 5). Small juveniles dominated in the surface waters, but larger individuals were generally found closer to the benthos (Fig. 5). During the night, the relative abundance of small individuals decreased at both depths. Close to the benthos an increase in large individuals was evident. There was no discernible pattern of vertical migration; however, combining data across months to increase the number of juveniles in the analysis removed the possibility of detecting vertical migration in any one month.

The number of *Photololigo* sp. A juveniles captured during the winter months was similar to most of the summer monthly catches (Fig. 6); although winter catches never reached levels such as those seen in December 1991 (Table 6). The large number of small juveniles captured over the winter (Fig. 6) indicates that *Photololigo* sp. A spawns and hatches in both seasons. A similar size range was captured at each sampling during the summer months (Fig. 7).

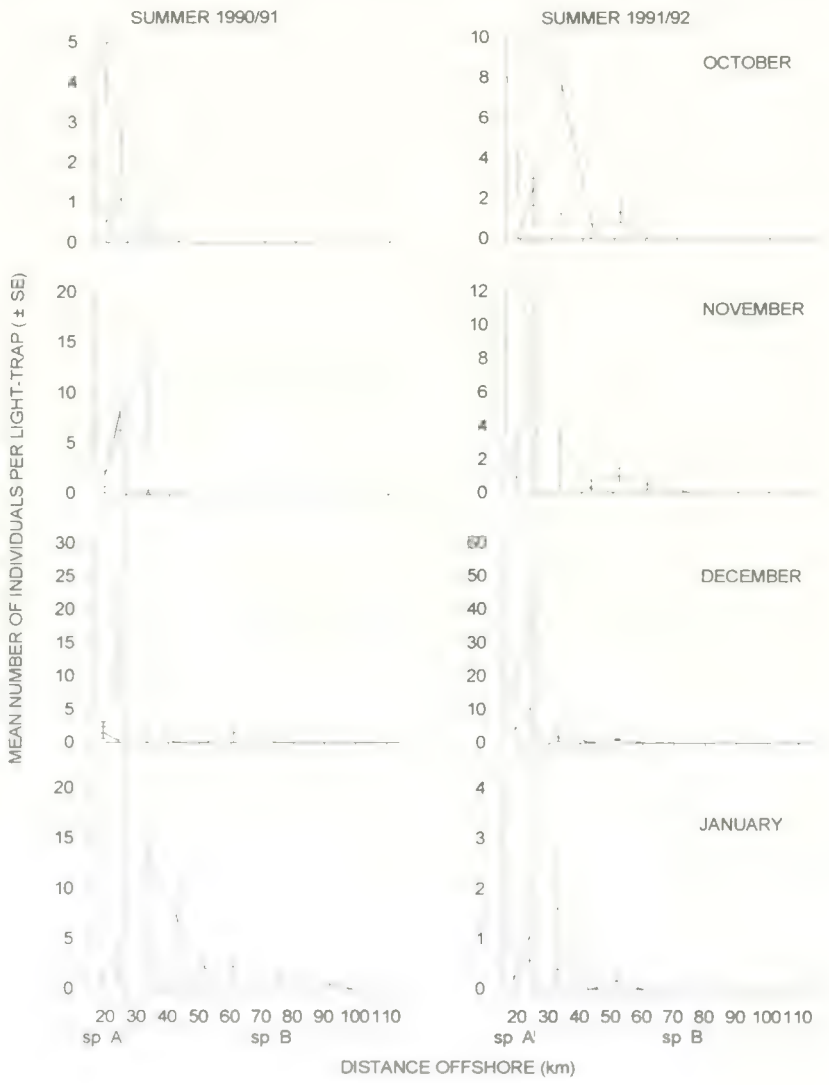

Figure 2

Catches of juvenile *Photololigo* sp. A (found at 19 and 24 km) and *Photololigo* sp. B (found at 33 km and greater) from Townsville, Australia. Most values are averages (± standard error) of six one-hour sets over three nights. See Table 1 for replicates at each station. (Solid lines, deep light-traps; dashed lines, shallow light-traps). Note the variable scale of the Y-axes.

Physical parameters

Both temperature and salinity decreased nonlinearly across the lagoon; discontinuities in both variables occurred midway across the Lagoon (Fig. 8). Temperature or salinity discontinuities were detected on at least six out of nine nights between the 33-km station and one or both of the neighbouring stations. This suggested that in the lagoon the water mass was heterogenous and may have influenced the distribution patterns of juvenile squid.

Salinity-temperature profiles of the water column at each station indicated thermoclines were present on some nights (Table 7). A thermocline was defined as a temperature change greater than 0.5°C between surface and bottom water; differences as great as 3°C were detected during January. However, these thermoclines were a temporally and spatially unstable feature of the water column, possibly due to variable wind conditions and the shallow body of water being sampled.

Discussion

Light-traps have provided a technique by which spatio-temporal distribution patterns of two *Pho-*

tololigo species can be described. Identification of *Photololigo* species using allozyme electrophoresis suggests that the two species are separated geographically across the Great Barrier Reef Lagoon (Yeatman and Benzie, in press). This separation occurs in a region of the coastal lagoon where temperature-salinity data indicate heterogeneity. High numbers of juvenile *Photololigo* sp. A at stations close to the mainland suggests that spawning grounds for this species may be close to the coast, a feature typical for loliginid squid (Mangold, 1987). Furthermore, the presence of small and large individuals during summer and winter months indicates that spawning, hatching, and recruitment are not seasonal events. This characteristic may be more common for tropical species that tend to have shorter lifespans than temperate species (Jackson and Choat, 1992). Large numbers of small juveniles collected during the winter may be a function of slower growth during the winter (Jackson and Choat, 1992). Little is known about *Photololigo* sp. B adults; however, the presence of juveniles in this region suggests that an adult population does occur in the Townsville region and that spawning occurs throughout the summer. The identification of juvenile *Photololigo* was confirmed on a subsample of specimens captured during the summer. Conclusions drawn from this study are based upon the assumption that the offshore distribution pattern of the two species was consistent in all other months of sampling.

Table 2

Catch per hour of light-trapping for each *Photololigo* species across the Great Barrier Reef Lagoon for eight months of summer sampling. *Photololigo* sp. A at stations 19 km and 24 km and *Photololigo* sp. B farther offshore.

	Species A		Species B				
Month	19km	24km	33km	43km	52km	61km	Total
1990							
Oct	2.38	1.81	0.25	0	0	0	0.62
Nov	0.75	8.25	5.42	—	0	0	2.88
Dec	1.88	8.00	0.50	0	0	0.75	2.63
1991							
Jan	0.42	1.33	9.42	3.58	1.00	1.13	2.91
Oct	1.67	2.17	4.25	0.25	0.67	0	1.50
Nov	1.83	4.83	2.17	0.42	0.50	0.25	1.67
Dec	10.67	24.42	1.92	0.17	0.50	0	6.28
1992							
Jan	0.83	1.75	1.67	0.17	0.08	0	0.75
Total	2.59	6.31	3.30	0.72	0.36	0.17	2.33

Table 3

Planned comparisons of juvenile *Photololigo* sp. A densities between depths, years, and sites.

Contrast	df	Contrast sums of squares	Mean squares	*F*-value	*P>F*
Depths	1	9.8165	9.8165	12.20	0.0006
Years	1	3.7565	3.7565	4.67	0.0320
Sites	1	8.6892	8.6892	10.80	0.0012
Residual	177	142.3838	0.8044		

Table 4

Planned comparisons of juvenile *Photololigo* sp. B densities between depths and years.

Contrast	df	Contrast sums of squares	Mean squares	*F*-value	*P>F*
Depths	1	17.0607	17.0607	37.85	0.0001
Years	1	0.0438	0.0438	0.10	0.7554
Residual	335	148.7448	0.4507		

Juvenile squid are not easily sampled with towed nets (Vecchione, 1979; Vecchione and Gaston, 1985; Holme, 1974). They have highly developed sensory and locomotor systems (Boletzky, 1974) and it is likely that these animals are often undersampled because of net avoidance. Choat et al. (1993) have shown that plankton nets select for small larval fish, but larger fish are captured from the same water column by using light attraction. Thorrold (1992), as well as this study, showed that light-traps are a useful technique for capturing juvenile squid. However, like most sampling techniques, the light-traps have biases. One problem is that light-traps sample an unknown volume of water. Nonetheless, they have

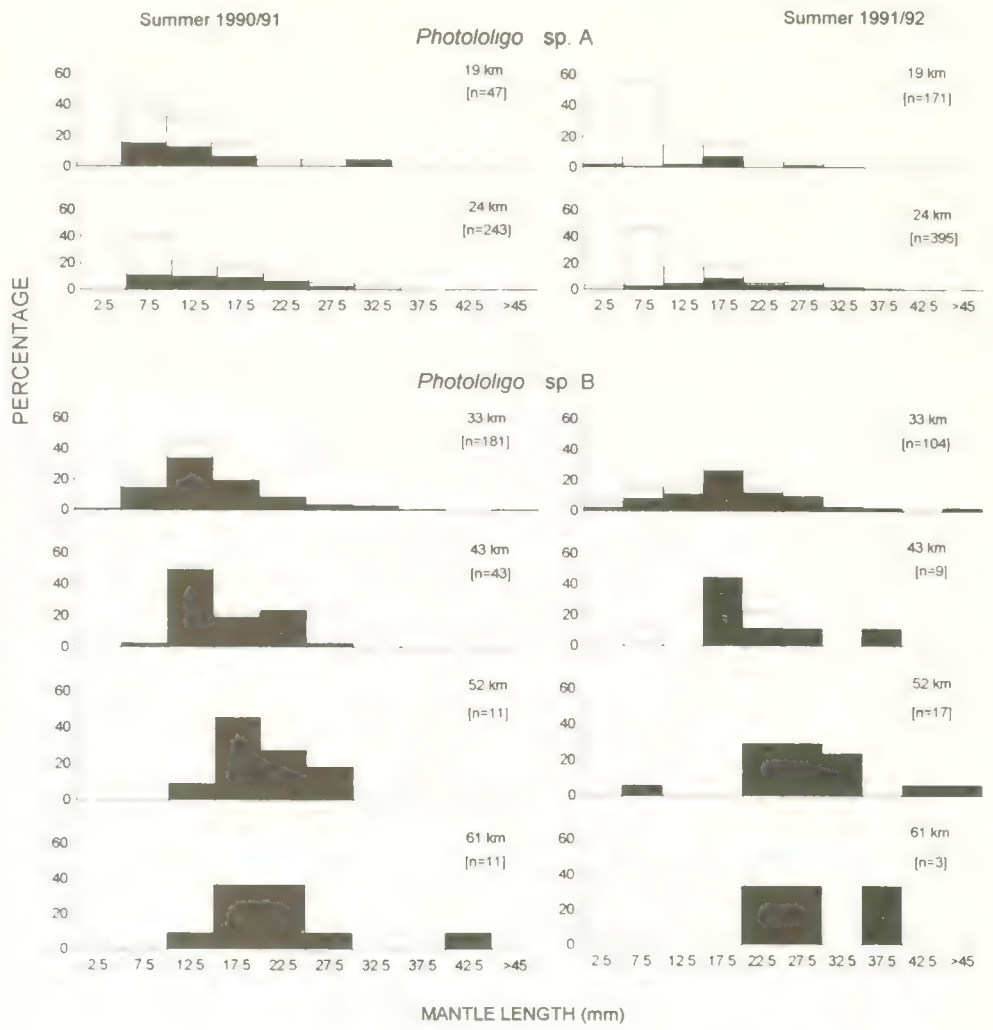

Figure 3

Size-frequency distribution of *Photololigo* sp. A and *Photololigo* sp. B caught at each station (pooled across months) in deep (shaded) and shallow (unshaded) light-traps. Total number of juveniles indicated in brackets.

Table 5

Results of the multiway frequency analysis to examine changes in the size distribution of *Photololigo* sp. A between time of night and depth.

Source	df	χ^2	P
Depth	1	92.8	0.00
Time	1	25.57	0.00
Depth × Time	1	0.19	0.66

been validated as useful devices for monitoring relative abundance patterns in larval supply of pelagic juvenile fish at fixed locations (Milicich et al., 1992). Great care needs to be exercised when interpreting catch rates from different locations because changes in water transparency can bias light-trap efficiency. Similarly, it is not possible to quantitatively compare catches from drifting and anchored light-traps (Thorrold, 1992). This is because the former act as lagrangian drifters and sample photopositive organisms from within a constant light pool. In contrast, the moored light-traps experience a variable water flow that may greatly increase the volume of water swept in an hour of sampling. Despite more intensive sampling on the reefs, catches of *Photololigo* were low and we conclude that spawning does not occur near the reefs and that juvenile *Photololigo* individuals are concentrated in the lagoon. In the

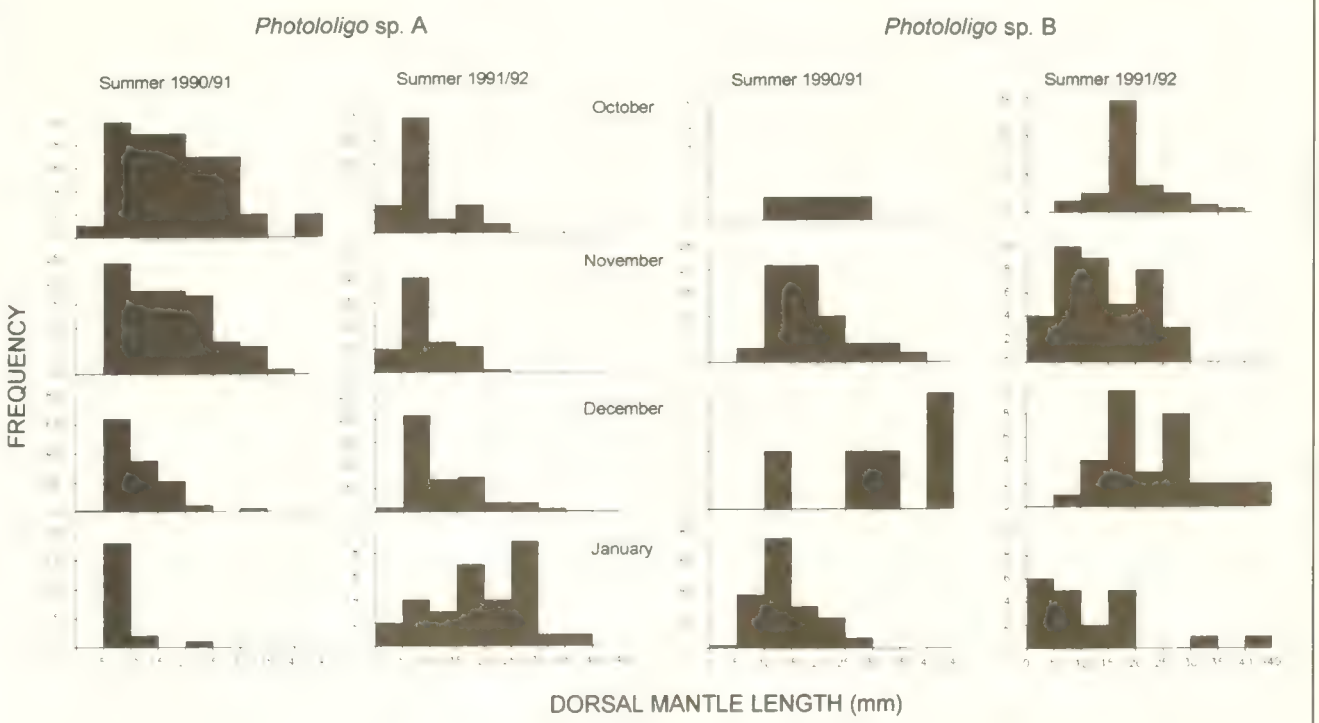

Figure 4

The size-frequency distribution of juvenile *Photololigo* sp. A and *Photololigo* sp. B during eight months of summer sampling. Size classes are mid-points of each class. Data are pooled across depths and stations.

present study, a gradient of turbidity across the shelf makes it possible that inshore catches would underestimate abundance if corrected for diminishing light-pools. However, if the error was significant, it would only exaggerate, not diminish, our observation that juvenile squid were more abundant within the coastal lagoon.

Table 6

Analysis of variance examining differences between densities of *Photololigo* sp. A at the 19 km station between summer months of 1990/91 and 1991/92 and winter months of 1991.

Source	df	Contrast sums of squares	Mean squares	*F*-value	*P>F*
Month	11	1118.200	101.654	9.55	0.0001
Residual	214	2277.910	10.644		

High catches of juvenile squid in the coastal lagoon were at locations where discontinuities were often observed in surface temperature and salinity. Hydrodynamic modelling of this region suggests that the coastal lagoon is often subject to velocity shear (King and Wolanski, 1992). Water in the lagoon typically flows southward under the influence of the poleward East Australian Current, which pushes water onto the outer shelf and through the reef matrix, especially through channels like the Magnetic Passage. Under typical south-easterly wind conditions the shallow body of water trapped against the coast moves in the opposite direction, northwards. The result is a velocity shear between the two water masses and a zone of low residual displacement. Modelling studies suggest that the cross-shelf location of this feature, referred to as a separation front (King and Wolanski, 1992), will shift seawards as the wind strength increases and vice versa. This mobility of the frontal region is consistent with the daily and monthly variability of salinity and temperature at the surface indicated by our physical monitoring during the second summer.

This low-shear zone is identified as a significant place for aggregation of planktonic organisms. Cross-shelf studies have shown highest abundances of larval reef fishes in a similar location near the

center of the Great Barrier Reef Lagoon (Thorrold, in press). These catches included individuals taken from reefs farther offshore, as well as piscivorous larvae of various scombrids from inshore (Thorrold, 1993). It is not clear whether aggregation of these stages is passive, due to hydrodynamics, or the result of attraction to the coastal boundary area by enhanced secondary productivity in this frontal zone (Thorrold and McKinnon, 1992). This discontinuity may be a mechanism separating the two *Photololigo* species geographically. The separation of juvenile cephalopod species in the Gulf Stream east of New England is thought to be closely related to mesoscale hydrological features (Vecchione and Roper, 1986). The importance of hydrological features in aggregating juvenile squid has been identified in a number of species (Rodhouse and Clarke, 1985; Brunetti and Ivanovic, 1992; Rodhouse et al., 1992). This suggests that these areas are ecologically important for juvenile squid.

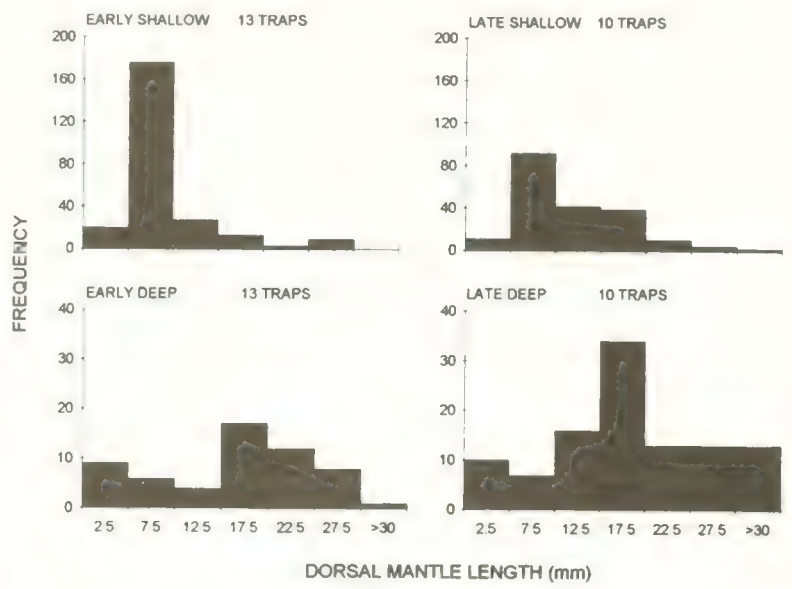

Figure 5

Size-frequency distributions of juvenile *Photololigo* sp. A from the two inshore stations at two sampling depths (pooled across the summer months 1991/92), captured early (before 2400 hr) and late (after 2400 hr) in the night.

The second way in which shelf-scale hydrodynamics affects the stability of the water column is the intrusion of upwelled waters from the shelf-break driven onto the shelf by variations in the speed and position of the East Australian Current. These cold intrusions can be tracked into the Great Barrier Reef Lagoon (King and Wolanski, 1992) and the strong thermal stratification observed in January 1992 was consistent with an intrusion at this time. A cold bottom layer at 33 km was evident on one night in November, but the inner stations were not stratified. The presence of juvenile *Photololigo* at most stations in all months, despite a range of physical conditions, suggests juvenile *Photololigo* can tolerate substantial environmental variation. This tolerance is consistent with a nonseasonal reproductive strategy, which is essential for a species that lives for only four months.

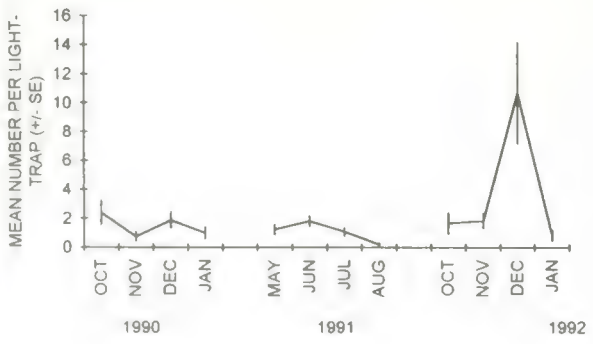

Figure 6

Catches of juvenile *Photololigo* sp. A at the 19-km station over twelve months: during summer 1990/91, winter 1991, and summer 1991/92. (Data pooled across depth and nights.)

During the night there was little evidence of a pronounced vertical migration such as the mass aggregations of juvenile *Loligo* spp. on the benthos (Vecchione and Gaston, 1985) or the general movement to the surface by juvenile *L. pealei* (Vecchione, 1981). The absence of vertical movement during the night suggests that the observed ontogenetic shift of *Photololigo* sp. B farther offshore and deeper is real and not a product of location confounded with time of night when sampling occurred. However, as was noticed in the catch-per-unit-of-effort values, both species are caught in relatively low numbers; hence, conclusions based on small differences that are not significantly different are limited. There was a problem with low numbers in all spatial and temporal trends described. However, this was a preliminary study with just two hours of sampling at each station per night. More intensive sampling in bound-

Table 7

Depth of the thermocline (m) at each station on each night of sampling during the three months of the 1991/92 summer.

Sampling period and situation	Depth of thermocline		
	Day 1	Day 2	Day 3
October 1991			
19 km	14	11	Absent
24 km	13	14	Absent
33 km	10	13	Absent
43 km	10	Absent	Absent
52 km	25	Absent	Absent
61 km	31	Absent	—
November 1991			
19 km	Absent	Absent	Absent
24 km	Absent	Absent	Absent
33 km	Absent	Absent	20
43 km	Absent	Absent	22
52 km	Absent	Absent	25
61 km	Absent	Absent	29
January 1992			
19 km	7	7	9
24 km	9	9	9
33 km	11	13	12
43 km	15	15	18
52 km	28	24	27
61 km	31	47	—

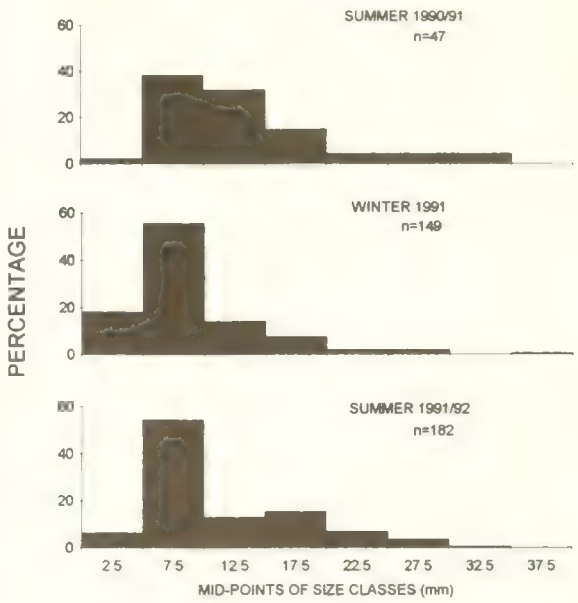

Figure 7

Size-frequency distributions of juvenile *Photololigo* sp. A at the 19-km station during the summer and winter months. (Numbers are pooled across months, depth, and nights.)

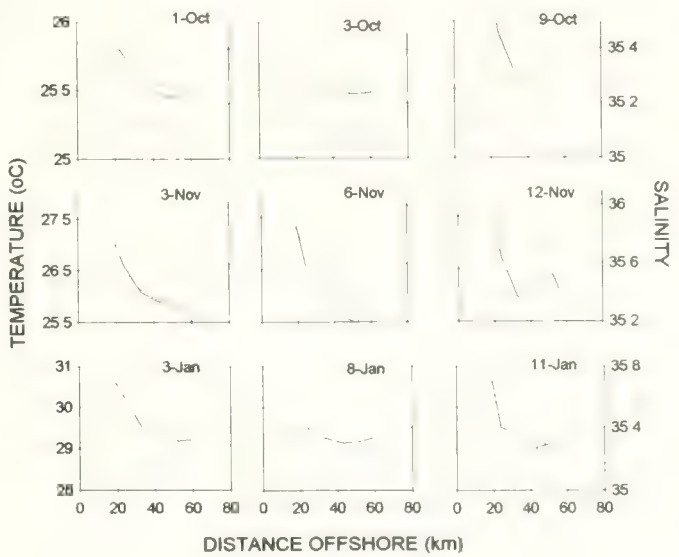

Figure 8

Surface temperature (dashed) and salinity (solid) profiles across the Great Barrier Reef Lagoon for each night of sampling in October and November 1991 and in January 1992. The Conductivity Temperature Device failed during the December cruise.

ary waters, both vertical and horizontal, is needed to understand how juvenile squid react to the physical environment. This study has shown that light-traps are useful devices for catching juvenile squid, providing a basis for a more intensive study of the early life-history of squid.

Acknowledgments

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Literature cited

Boletzky, S. v.
1974. The 'larvae' of Cephalopoda: a review. Thalassia Jugoslavica 10:45–76.
1977. Post-hatching behaviour and mode of life in cephalopods. Symp. Zool. Soc. Lond. 38:557–567.

Boyle, P. R.
1990. Cephalopod biology in the fisheries context. Fish. Res. 8:303–321.

Brunetti, N. E., and M. L. Ivanovic.
1992. Distribution and abundance of early life stages of squid (*Illex argentinus*) in the south-west Atlantic. ICES J. mar. Sci. 49:175–183.

Choat, J. H., P. J. Doherty, B. A. Kerrigan, and J. M. Leis.
1993. A comparison of towed nets, purse seine, and light-aggregation devices for sampling larvae and pelagic juveniles of coral reef fishes. Fish. Bull. 91:195–209

Day, R. W., and G. P. Quinn.
1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59:433–463

Doherty, P. J.
1987. Light-traps: selective but useful devices for quantifying the distributions and abundances of larval fishes. Bull. Mar. Sci. 41:423–431.

Holme, N. A.
1974. The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. J. mar. biol. Assoc. U.K. 54:481–503.

Jackson, G. D., and J. H. Choat.
1992. Growth in tropical cephalopods: an analysis based on statolith microstructure. Can. J. Fish. Aquat. Sci. 49:218–228.

King, B., and E. Wolanski.
1992. Coastal dynamics along a rugged coastline. *In* D. Prandle (ed.), Dynamics and exchanges in estuaries and the coastal zone, p. 577–598. Coastal and Estuarine Studies 74, Springer-Verlag.

Mangold, K.
1987. Reproduction. *In* P. R. Boyle (ed.), Cephalopod life cycles. Vol 2: Comparative reviews, p. 157–200. Academic Press, NY.

Milicich, M. J.
1992. Light-traps: a novel technique for monitoring larval supply and replenishment of coral reef fish populations. Unpubl. Ph.D. thesis, Griffith University, 127 p.

Milicich, M. J., M. G. Meekan, and P. J. Doherty.
1992. Larval supply: a good predictor of recruitment of three species of reef fish (Pomacentridae). Mar. Ecol. Prog. Ser. 86:153–166.

Rodhouse, P. G., and M. R. Clarke.
1985. Growth and distribution of young *Mesonychoteuthis hamiltoni* Robson (Mollusca: Cephalopoda): an Antarctic squid. Vie Milieu 35:223–230.

Rodhouse, P. G., C. Symon, and E. M. C. Hatfield.
1992. Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. Mar. Ecol. Prog. Ser. 89:183–195.

Thorrold, S. R.
1992. Evaluating the performance of light traps for sampling small fish and squid in open waters of the central Great Barrier Reef lagoon. Mar. Ecol. Prog. Ser. 89:277–285.
1993. Post-larval and juvenile scombrids captured in light traps: preliminary results from the central Great Barrier Reef lagoon. Bull. Mar. Sci. 52:631–641.
In press. Coupling of pre-settlement reef fish distribution and hydrography in the central Great Barrier Reef lagoon. Proc. Seventh International Coral Reef Symposium, 1992.

Thorrold, S. R., and A. D. McKinnon.
1992. Biological significance of the coastal boundary layer off Townsville, North Queensland. *In* D. A. Hancock (ed.), Larval biology. Australian Society for Fish Biology Workshop, Hobart 1991. Bureau of Rural Resources Proceedings 15:104–109.

Vecchione, M.
1979. Larval development of *Illex* Steenstrup, 1880, in the northwestern Atlantic, with comments on *Illex* larval distribution. Proc. Biol. Soc. Wash. 91:1060–1075.
1981. Aspects of the early life history of *Loligo pealei* (Cephalopoda; Myopsida). J. Shellfish Res. 1:171–180.
1987. Juvenile ecology. *In* P. R. Boyle (ed.), Cephalopod life cycles. Vol 2: Comparative reviews, p. 61–84. Academic Press, NY.

Vecchione, M., and G. R. Gaston.
1985. In-situ observations on the small-scale distribution of juvenile squids (Cephalopoda: Loliginidae) on the northwest Florida shelf. Vie Milieu 35:231–235.

Vecchione, M., and C. F. E. Roper.
1986. Occurrence of larval *Illex illecebrosus* and other young cephalopods in the slope water/Gulf Stream interface. Proc. Biol. Soc. Wash. 99:703–708.

Voss, G. L.
1983. A review of cephalopod fisheries biology. Mem. Natl. Mus. Victoria 44:229–241.

Yeatman, J., and J. A. H. Benzie.
In press. Genetic structure and distribution of *Photololigo* in Australia. Mar. Biol.

Young, R. E., and R. F. Harman.
1988. "Larva," "paralarva," and "subadult" in cephalopod terminology. Malacologia 29:201–207.

Abstract.— The distribution and activities of rockfish, *Sebastes* spp., inhabiting depths between 21 and 150 m in the coastal fjord of Saanich Inlet, British Columbia, were assessed by using the *Pisces IV* submersible. Quillback rockfish, *S. maliger*, was the numerically dominant rockfish, attaining a median density of 5.7 fish·100m^{-2} between 21 m and 100 m of depth. Copper rockfish, *S. caurinus*, tiger rockfish, *S. nigrocinctus*, yellowtail rockfish, *S. flavidus*, yelloweye rockfish, *S. ruberrimus*, and green-striped rockfish, *S. elongatus*, were all observed in consistently low densities (<1 fish·100m^{-2}). The greatest densities of rockfish occurred over complex habitat of broken rock and boulders. The majority (>50%) of rockfish were observed either perched on open substrate, hovering, or swimming. All rockfish species were observed near quillback rockfish (>75% occurrence); and quillback, copper, and yellowtail rockfishes were also found in association with conspecifics.

Observations on the distribution and activities of rockfish, *Sebastes* spp., in Saanich Inlet, British Columbia, from the *Pisces IV* submersible

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Prior to the advent of submersibles, in situ observations of deep-water demersal fish assemblages were constrained by time-depth limitations of SCUBA, which restrict observations of fish assemblages primarily to depths above 40 m (130 ft) (e.g. Moulton, 1977; Larson, 1980; Hallacher and Roberts, 1985; Richards, 1987; Murie, 1991). Distributional studies of fishes inhabiting waters deeper than 30–40 m have therefore relied on hook-and-line surveys, box trapping, or net trawling, all of which have known biases and limitations (Westrheim, 1970; Uzmann et al., 1977; Krieger, 1993). The recent availability of small submersibles for research purposes has allowed direct visual assessment of the depth distribution, density, and habitat of a variety of deep-water fish species (Uzmann et al., 1977; Carlson and Straty, 1981; Richards, 1986; Dennis and Bright 1988; Pearcy et al., 1989; Stein et al., 1992; Krieger, 1993).

Rockfish (*Sebastes* spp.) are important to nearshore recreational and commercial fisheries along the northeastern Pacific coast (Patten, 1973; Richards, 1987). Many inshore rockfish species are believed to be ecologically and morphologically similar, and are primarily benthic, sedentary fishes (Patten, 1973; Moulton, 1977; Mathews and Barker, 1983; Richards, 1986, 1987; Murie, 1991). Distributions of nearshore rockfish may depend on a variety of factors, including depth, habitat, and the presence of con- and hetero-specifics. Various species are known to segregate bathymetrically (Larson, 1980; Hallacher and Roberts, 1985; Richards, 1986, 1987; Pearcy et al., 1989), reducing or eliminating the potential for competitive interactions between otherwise ecologically similar species (Larson, 1980). Using a submersible, it is possible to observe directly the species-specific depth distributions, as well as to estimate each species' numerical abundance or density with depth. Changes in density with depth within a rockfish species may ultimately be related to fish size because rockfish size is often posi-

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tively correlated with depth (Westrheim, 1970; Boehlert, 1980; Wilkins, 1980; Richards, 1986).

Nearshore rockfish are usually found in close association with the substrate or vertical relief (e.g. kelp beds) and their density may be dependent on the type of habitat available (e.g. boulder fields, shelter holes, etc.) (Patten, 1973; Moulton, 1977; Richards, 1986, 1987; Pearcy et al., 1989; Stein et al., 1992). Depth and density distributions of nearshore rockfish in British Columbia have been assessed primarily by hook-and-line surveys (e.g. Richards et al., 1988) and observations from submersibles are lacking. To date, only one study has assessed the distribution of nearshore rockfish in British Columbia using direct observations from a submersible (Richards and Cass, 1985; Richards, 1986). In their study, the depth and habitat distributions of rockfish were surveyed at depths of 21–140 m in coastal waters of the northeastern Strait of Georgia. In addition to observations on depth and type of habitat frequented by various rockfish species, however, submersibles also provide a unique opportunity to observe the behavioral activities of the fishes and their associations with conspecifics and heterospecifics. To date, there has been a lack of submersible studies that attempt to quantitatively assess the in situ activities of rockfish.

In the present study, we examined the distribution of rockfish observed from a submersible deployed in Saanich Inlet, a coastal fjord in the southern Strait of Georgia, British Columbia (Fig. 1). Fjords in British Columbia differ from open coastal areas, such as those surveyed by Richards (1986), in that they typically rely on estuarine-type circulation for mixing but have submerged sills which restrict mixing of waters below the sill depth (Thomson, 1981). For fjords of Vancouver Island, B.C., limited circulation results in low dissolved oxygen levels in relatively deep water (Pickard, 1963). In Saanich Inlet, restricted mixing at depth results in oxygen-deficient waters (<2.0 $mg \cdot L^{-1}$) below 100 m throughout most of the year and intermittent, seasonal (usually during January–August) anoxia with production of hydrogen sulfide (Herlinveaux, 1962; Liu, 1989), which is toxic to aerobic organisms (Martin et al., 1981). Various studies of invertebrates in Saanich Inlet have shown that the concentration of dissolved oxygen in the water limits their depth distribution (e.g. Burd, 1983; Mackie and Mills, 1983; Jamieson and Pikitch, 1988; Liu, 1989). Field studies have also demonstrated that the vertical or horizontal distribution of fishes is positively correlated with oxygen concentration (reviewed in Kramer, 1987). We therefore speculated that depth distributions for rockfish species in Saanich Inlet would be relatively shallow when compared to their reported maximum depths in open coastal areas.

The present study is the first to examine in situ species composition and density of rockfish in a coastal fjord in British Columbia. In addition, in situ behavioral activities and species associations of nearshore rockfish at depths greater than 30 m in coastal waters of British Columbia have been described for the first time.

Methods

The *Pisces IV* submersible (Department of Fisheries and Oceans, Canada) was used to survey rockfish populations in Saanich Inlet on 9–10 December 1986. A comprehensive description of the *Pisces IV* submersible was given by Mackie and Mills (1983). The inlet has a steep, rocky slope bottom interspersed with sand-shell valleys and is 7.2 km at its

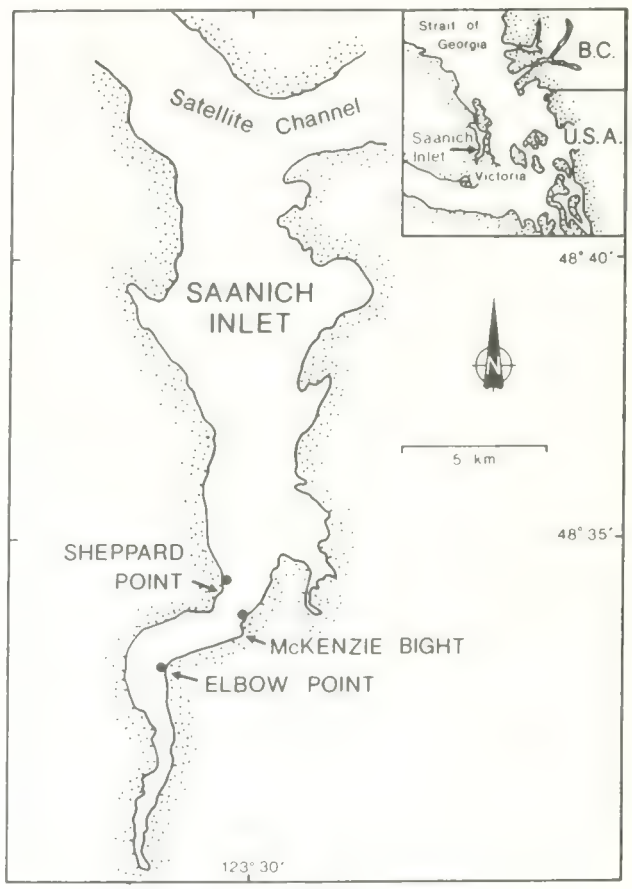

Figure 1

Location of transect sites (•) in Saanich Inlet, Vancouver Island, British Columbia. Inset: Location of Saanich Inlet in relation to the mainland of B.C.

widest. Specifics of the oceanographic characteristics of Saanich Inlet are detailed elsewhere (Herlinveaux, 1962; Anderson and Devol, 1973). Of relevance is that the basin of the inlet reaches a maximum depth of 234 m, but a submerged sill at 75 m at its mouth in Satellite Channel restricts the renewal of deep-water into the inlet. The resulting oxygen deficiency, anoxia, and production of hydrogen sulfide is offset in some years when well-oxygenated, dense bottom-water intrudes over the sill (Herlinveaux, 1962; Anderson and Devol, 1973). We therefore did a hydrocast at depths of 0–225 m to determine the depth of the oxycline in the inlet and whether hydrogen sulfide was present at the time of the surveys. The sampling station was located at lat. 48°37.80'N and long. 123°30.00'W (Liu, 1989).

Three sites within Saanich Inlet were surveyed: five transects were traversed at Elbow Point, eight in an area north of McKenzie Bight, and three in an area north of Sheppard Point (Fig. 1). These areas were known from preliminary SCUBA dive surveys to have rockfish present in >30 m water depth (Murie et al., pers. obs.). All surveys were conducted during daylight hours (09:30 hours to 16:00 hours) and were also restricted to a depth range between 20 and 150 m because the buoyancy of the *Pisces IV* is not finely controlled above 20 m, and bottom time restrictions precluded the transects starting at the basin floor (~200 m). Depth at which each transect started therefore varied among sites owing to slope and positioning of the submersible, with starting depths of 95–109 m at Elbow Point, 92–154 m at McKenzie Bight, and 67–74 m at Sheppard Point.

At the start of each transect, the *Pisces IV* submerged in open water and on reaching depth the external floodlights were lit and the submersible was manoeuvred horizontally, slowly, toward the cliff face. Once the bottom substrate (cliff) was located, the submersible began a slow vertical ascent (~5 $m \cdot min^{-1}$), keeping the viewing ports (port, pilot, and starboard) directed perpendicular to and approximately 3 m from the substrate. Underwater visibility at the time of the surveys was ~5–6 m with external illumination.

On ascent, an audio-record was made of the species, time, depth, estimated size (whenever possible), activity, and habitat for each rockfish observed. Each observer (port and starboard) recorded all rockfish encountered within a plane bisecting the pilot's viewport and extending outward at an angle of approximately 45°, corresponding to approximately 3 m of horizontal distance across the substrate (i.e. viewing width). To avoid counting the same fish twice, any rockfish swimming across the path of the submersible or positioned close to the pilot's viewing area was pointed out to the other observer. Size was visually estimated (±5 cm) by comparing the fish with an externally mounted graduated rod. Rockfish were designated as small (≤20 cm total length [TL]) and large (>20 cm TL); large referring to the size at which they enter recreational and commercial fisheries (Richards, 1986). Activity of each fish was scored according to whether the fish was perched in the open, positioned in a crevice, occupying a shelter hole, hovering off the substrate, or swimming. Habitat was categorized as vertical wall (may have cracks, small crevices, or ledges; score=1), complex (comprising broken rock and boulder fields; score=2), or sand-mud (score=3). Any change in the habitat or slope of the substrate (±10°) was recorded and the depth noted.

Rockfish density was estimated for each habitat type over 20–m depth intervals. The total number of fish recorded by both observers within each habitat type over a 20–m depth interval was divided by the total area of that habitat type viewed over the depth interval. The area viewed was calculated by multiplying the viewing width of both observers (i.e. 6 m) by the ratio of the change in depth to the sine of the slope.

Median densities of small and large fish were calculated for each habitat type and 20–m depth interval, with transects pooled for increased sample size. Density distributions for rockfish were skewed so densities were calculated as medians with 25% and 75% quartiles. Densities of quillback rockfish, *S. maliger*, among depth intervals and habitats were analyzed by using Kruskal-Wallis tests (SAS, 1985), as this species had an adequate median density (>1 fish·$100m^{-2}$). Statistical significance was indicated by $P \leq 0.05$. Analyses for the other rockfish species (median densities <1 fish·$100m^{-2}$) were limited to qualitative comparisons of their depth distributions and numerical abundances.

Activity of each species of rockfish was analyzed using percent occurrence, which was calculated by dividing the sum of all individuals observed in each activity by the total number of individuals of the species for which activities were recorded, and multiplying by 100%. Species associations were determined for individual fish of each species by scoring the presence of a conspecific or a heterospecific within 3 m. The sum of the number of individuals which were observed in the presence of a con- or hetero-specific was then expressed as a percentage of the total number of individuals of the species. Individual rockfish with no other rockfish within 3 m were considered to be 'alone' (solitary).

Results

Physical habitat

An area of approximately 10,521 m^2 was surveyed from the submersible, of which 38% was wall, 47% complex, and 15% sand-mud habitat. Area of coverage among habitat types differed with depth (Fig. 2). The area of complex and sand-mud habitat covered in the surveys decreased with depth whereas that of wall habitat increased. Sand-mud habitat was encountered only at depths of <60 m and the median area surveyed among transects was zero. Wall habitat was the only habitat type observed at depths greater than 120 m. The slope of the substrate was correlated with depth (Spearman rank correlation: r_s=0.37, P<0.001) and habitat (r_s =-0.71, P<0.001). This was evident in that wall habitat found primarily in deep water provided vertical or near-vertical relief (~70–90° slope), whereas complex and sand-mud habitats in shallower depths provided a graded substrate (~20–70° slope).

The area of each type of habitat surveyed differed among survey sites (Kruskal-Wallis: P=<0.001, 0.03, and <0.001 for wall, complex, and sand-mud habitat respectively). Elbow Point and McKenzie Bight had similar habitats whereas Sheppard Point had less wall and complex habitat and more sand-mud habitat than the Elbow Point and McKenzie Bight sites.

At the time of the surveys, Saanich Inlet was not anoxic although waters below 100 m were deficient in dissolved oxygen (Liu, 1989) (Table 1). Hydrogen sulfide was not present at any depths sampled in the inlet. Temperature and salinity were relatively stable below depths of 100 m.

Depth, size, and density distributions

Quillback rockfish represented 88% (681/770) of all rockfish sighted and were observed at a median depth of 54 m (Table 2). Density of quillback rockfish did not differ among depth intervals between 21–100 m (P=0.35) (Fig. 3A). Only three quillback rockfish were seen at depths >100 m. In total, the median size of 460 quillback rockfish was 23 cm (Table 2). Quillback rockfish size was positively correlated with depth (r^2=0.23, P<0.001, n=460) and the density of small and large quillback rockfish varied among depth intervals (P=0.01 and P=0.02 respectively) (Fig. 3B). Density of small quillback rockfish was similar to that of large quillback rockfish in the 21–40 m depth interval (P=0.66), but it was less at depth intervals greater than 40 m (all P<0.05) (Fig. 3B). In contrast, the median density of large quillback rockfish at depth intervals between 41–100 m was greater than their density in the 21–40 m depth interval (Fig. 3B).

Tiger rockfish, *S. nigrocinctus*, copper rockfish, *S. caurinus*, yellowtail rockfish, *S. flavidus*, green-striped rockfish, *S. elongatus*, and yelloweye rockfish, *S. ruberrimus*, all had median densities of zero in 21–150 m depths in Saanich Inlet (Table 2).

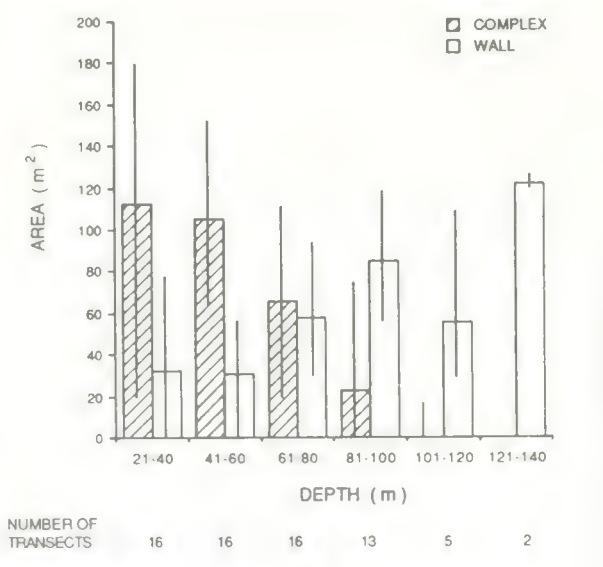

Figure 2

Overall median area of survey coverage for complex and wall habitat in relation to depth. Vertical bars represent the interquartile ranges ($Q_{0.25}$ to $Q_{0.75}$). Median area of sand-mud habitat surveyed was zero.

Table 1

Temperature, salinity, and dissolved oxygen measured throughout depths in Saanich Inlet on 12 December 1986. Hydrogen sulfide was not present at any of the depths sampled.

Depth (m)	Temperature (°C)	Salinity (‰)	Dissolved oxygen (mg L^{-1})
0	6.24	26.68	7.01
10	8.70	30.18	5.83
30	8.94	30.31	4.50
50	9.40	30.56	3.80
75	9.19	30.96	2.80
100	9.19	31.25	1.39
125	9.23	—	0.41
150	9.28	31.44	0.50
175	9.27	—	0.87
200	9.29	31.47	1.70
225	9.29	—	1.75

Table 2

Numerical abundance, median density, median depth, and median estimated size of *Sebastes* species observed at depths of 21–150 m in Saanich Inlet from the *Pisces IV* submersible.

		Density (fish·100m^{-2})		Depth (m)		Size (cm)	
Species	Number	Median	Range	Median	Range	Median	Range
S. maliger	681	5	(0–31)	54	(21–115)	23	(5–41)
S. nigrocinctus	28	0	(0– 2)	55	(33– 97)	28	(20–46)
S. caurinus	24	0	(0– 4)	44	(21– 65)	25	(5–36)
S. flavidus	23	0	(0– 7)	49	(41– 65)	35	(20–40)
S. elongatus	8	0	(0– 1)	65	(52–114)	18	(15–23)
S. ruberrimus	5	0	(0– 4)	89	(76–103)	28	(18–46)
Unidentified sp.	1			42		–	

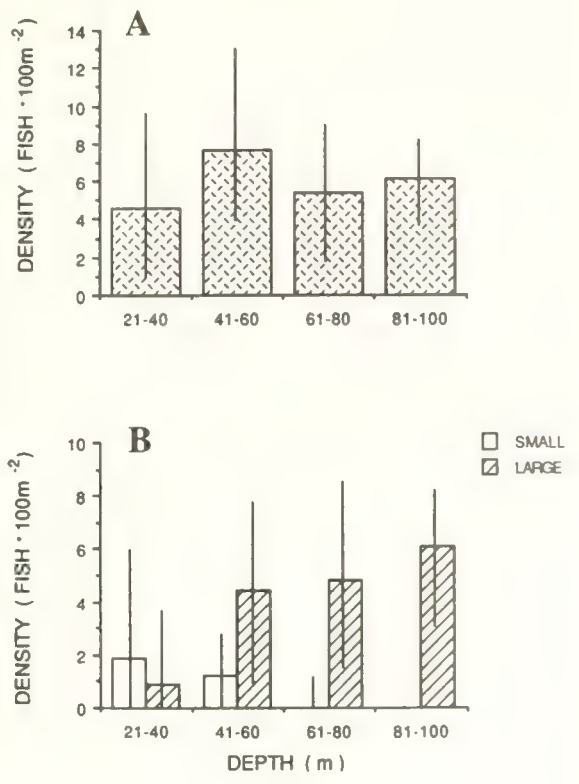

Figure 3

(**A**) Overall median densities of all quillback rockfish, *Sebastes maliger*, over depth; and (**B**) median densities of small and large quillback rockfish over depth. Vertical bars represent the interquartile ranges ($Q_{0.25}$ to $Q_{0.75}$). Median density of quillback rockfish in depths >100 m was zero.

Tiger rockfish accounted for 4%, and copper rockfish 3%, of the rockfish encountered; both were most abundant in 41–60 m (0.6 fish·100m^{-2}). Yellowtail rockfish also represented 3% of all rockfish observed with their density reaching a maximum of 6.3–6.6 fish·100m^{-2} in the 41–80 m depth intervals. Greenstriped rockfish (n=8), yelloweye rockfish (n =5), and one unidentified rockfish each represented less than 1% of all observed rockfish. Greenstriped and yelloweye rockfish both occurred in relatively deeper waters (Table 2).

The size of tiger rockfish was not correlated with depth (P=0.27, n=15) and only relatively large fish were seen from the submersible (Table 2). Copper rockfish size was positively correlated with depth (r^2=0.36, P=0.02, n=15), and no small copper rockfish were seen at depths greater than 40 m. Yellowtail rockfish seen were all relatively large fish (Table 2) and their size was not correlated with depth (P=0.46, n=21). All greenstriped rockfish observed were small (Table 2). Two juvenile yelloweye rockfish (18–20 cm TL) were observed at depths greater than 95 m and three subadult and adult yelloweye rockfish (36–46 cm TL) occurred between 80 and 90 m.

Habitat distribution

Density of quillback rockfish differed among survey sites (P=0.001). Densities observed at the Elbow Point and McKenzie Bight sites were similar (P=0.236), with a pooled median density of 5.7 fish·100m^{-2}. In contrast, the median density of quillback rockfish at Sheppard Point was zero.

Overall, quillback rockfish density was highest in areas of complex habitat (5.8 fish·100m^{-2}), followed

by wall habitat (3.5 fish·100m^{-2}) (Fig. 4). Only four quillback rockfish were observed over sand-mud habitat. Quillback rockfish densities, whether in complex or wall habitat, did not differ among depth intervals ≤100 m (P=0.52 and P=0.64 respectively) (Fig. 4).

Tiger, copper, yellowtail, and yelloweye rockfish were observed only over complex or wall habitats, whereas greenstriped rockfish occurred mostly over sand-mud habitat (Table 3). Tiger rockfish tended to occur in both complex and wall habitats, whereas copper, yellowtail, and yelloweye rockfish were seen mostly in complex habitat.

Activities

Quillback, copper, and greenstriped rockfish did not appear to be attracted to or obviously repelled by the presence of the submersible and its lights. At times, rockfish actively finned to maintain station after the submersible had produced currents. Any observed movements away from or towards the submersible were always relatively slow and, at times, hovering quillback rockfish would move slightly away from the path of the submersible, stop, and then resume hovering. Tiger and yelloweye rockfish appeared to have a delayed response to the submersible, in that it was possible to observe them prior to their actually moving into a shelter hole or crevice. In contrast, some spotted ratfish, *Hydrolagus colliei*, and a sixgill shark, *Hexanchus griseus*, were obviously attracted to the *Pisces*. These fish swam back-and-forth around the front of the submersible, repeatedly approaching the viewing ports near the external lights.

Activities were determined for a total of 662 quillback rockfish and the majority were observed hovering or perched on substrate in the open (Fig. 5), regardless of depth interval (all P>0.10). Copper rockfish were also observed primarily hovering and perched in the open, but were seen swimming more frequently than quillback rockfish. Both species were observed infrequently in crevices and rarely in shelter holes. Tiger rockfish were also observed most frequently perched in the open or occupying crevices. Yellowtail rockfish were all observed either hovering or swimming close to the substrate. All eight greenstriped rockfish were observed perched on the substrate. Of the five yelloweye rockfish observed, one was in a shelter hole, three were in crevices, and one was hovering.

Table 3

Numerical abundance of rockfish (*Sebastes* spp.) observed in densities of ≤1 fish·100m^{-2} over complex, wall, and sand-mud habitat in Saanich Inlet.

Species	Complex	Wall	Sand-Mud
S. nigrocinctus	13	15	0
S. caurinus	20	4	0
S. flavidus	21	2	0
S. elongatus	0	1	7
S. ruberrimus	4	1	0

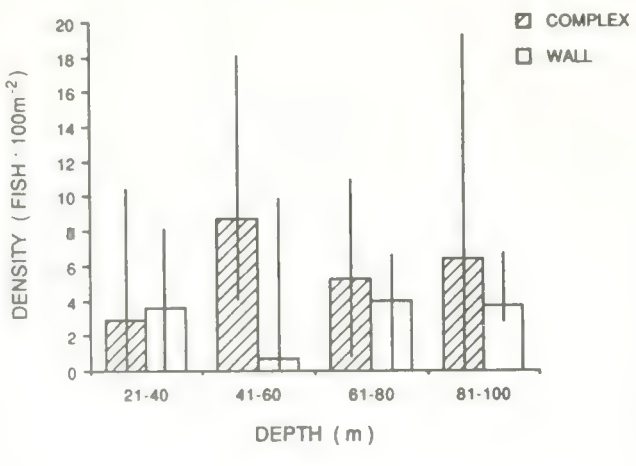

Figure 4

Median densities of quillback rockfish, *Sebastes maliger*, in complex and wall habitats among depths. Vertical bars represent interquartile ranges ($Q_{0.25}$ to $Q_{0.75}$). Median densities of quillback rockfish over sand-mud habitat were zero.

Species associations

The majority of quillback rockfish (94% occurrence) were observed within 3 m of at least one other quillback rockfish (Fig. 6). Quillback rockfish were almost never observed alone (2%) and were observed in the presence of other species relatively infrequently (~20% occurrence or less). Quillback rockfish formed loose conspecific aggregations that were distinctly different from the conspecific schools of yellowtail rockfish observed from the *Pisces*. When schooling, yellowtail rockfish formed tight groups of fish that orientated and moved together in the same direction, whereas in the aggregations of quillback rockfish, individual fish were orientated in various directions and engaged in various activities. Small groups of quillback rockfish (2–5 fish) observed from the submersible were interspersed between larger aggregations of more than 15 fish. Copper rockfish occurred within 3 m of quillback rockfish 92% of the time (Fig. 6), but also tended to occur near other copper rockfish

(64% occurrence) and tiger rockfish (32%). Copper rockfish, while usually near quillback rockfish, were also observed in conspecific aggregations and they were seldom seen alone (4%). Tiger rockfish were almost always observed near quillback rockfish (96% occurrence) and, to a much lesser extent, near other tiger rockfish (21%) (Fig. 6). The majority of yellowtail rockfish were observed in proximity to quillback rockfish (96%) and other yellowtail rockfish (91%). All five of the yelloweye rockfish seen were near quillback rockfish. Six greenstriped rockfish were observed near quillback rockfish whereas two were alone.

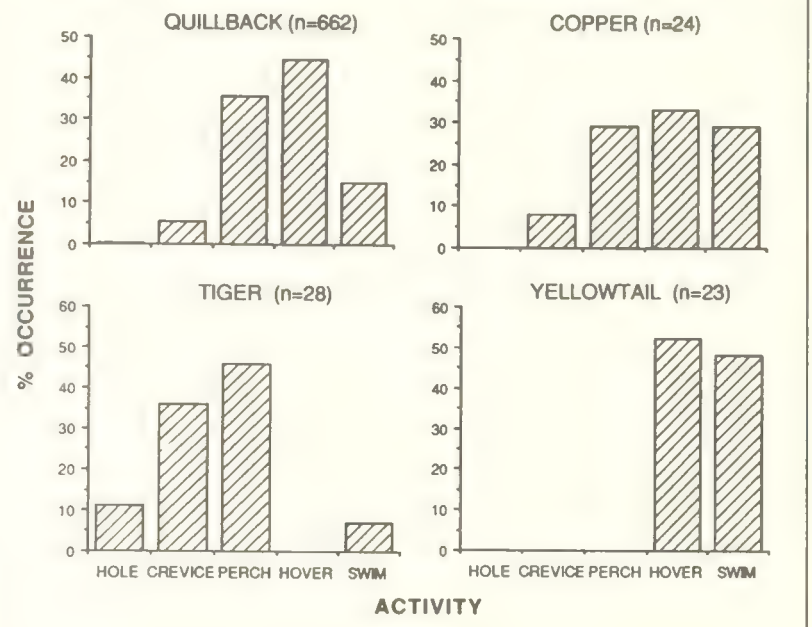

Figure 5

Percent occurrence of behavioral activities for quillback rockfish, *Sebastes maliger*; copper rockfish, *S. caurinus*; tiger rockfish, *S. nigrocinctus*; and yellowtail rockfish, *S. flavidus*, observed in Saanich Inlet from the *Pisces* submersible.

Discussion

Quillback rockfish are the numerically dominant rockfish species at depths of 21–100 m in nearshore areas of southern British Columbia, based on submersible observations in a fjord (this study) and in relatively open coastal areas (Richards, 1986). Based on both of these submersible studies, the main depth distribution of quillback rockfish is between 41 and 60 m, and their density at this depth is more than eight times greater than that of any other rockfish species observed at 41–60 m (Fig. 3A; Richards, 1986). As in Saanich Inlet, greenstriped and yelloweye rockfish were also observed in relatively low densities in the northeastern Strait of Georgia (means of ≤2 fish·100m^{-2} in various habitat types) (Richards, 1986), as well as tiger and copper rockfish (Richards and Cass, 1985). Yellowtail rockfish were not seen during submersible dives in the northeastern Strait of Georgia (Richards and Cass, 1985). In Saanich Inlet, complex habitat dominated by broken rock and boulder fields appears to be a common feature for the occurrence of the majority of these rockfish species. Based on *Pisces* surveys in the northeastern Strait of Georgia, Richards (1986) also observed that quillback and yelloweye rockfish were most abundant in complex habitat. Similarly, densities of copper and quillback rockfish were highest in complex habitat or in areas of highly irregular relief in Saanich Inlet in <40 m depth (Murie, 1991) and in the northern Strait of Georgia in <18 m depth (Richards, 1987). In SCUBA surveys, Matthews (1990) found the greatest densities of large copper and large quillback rockfish on high-relief rocky reefs in Puget Sound, Washington. Additionally, submersible observations in the vicinity of Heceta Bank, Oregon (Pearcy et al., 1989), suggested that tiger, yelloweye, and yellowtail rockfish were most frequently encountered over rock and rubble habitat. The densities of these near-bottom species may be greatest in this type of habitat because of increased protection from predators or increased density of prey due to the increase in microhabitat and vertical structure.

Stein et al. (1992) observed fish from a submersible at Heceta Bank and determined that the occurrence of fish species was related to specific substrates. Given the propensity of quillback rockfish to aggregate over complex habitat, differences in their density among sites surveyed in our study was not surprising. Sheppard Point, which had more sand-mud areas and a shallower slope, was noticeably different from Elbow Point and McKenzie Bight. It was also the only site where greenstriped rockfish were observed, which is consistent with the apparent habitat distribution of this species (Richards, 1986; Pearcy et al., 1989; Stein et al., 1992).

The overlap in the depth ranges, as well as the similarity in the median depths and the occurrence of fish over complex and wall habitats, suggested that quillback, copper, tiger, and yellowtail rockfish do not segregate in Saanich Inlet within the range

of bathymetry or habitat surveyed from the submersible. Yellowtail rockfish may be segregated spatially from tiger rockfish and, to some degree, copper and quillback rockfish, because the activities of yellowtail rockfish consistently placed them in the water column near the substrate but never in direct contact with the bottom. The appearance of quillback and copper rockfish near to one another (Fig. 6) was consistent with observations from SCUBA dive surveys at Saanich Inlet in 20–40 m. Sympatric aggregations of quillback and copper rockfish over complex habitat in Saanich Inlet can be dense (~25–50 fish·100m^{-2}) (Murie, 1991).

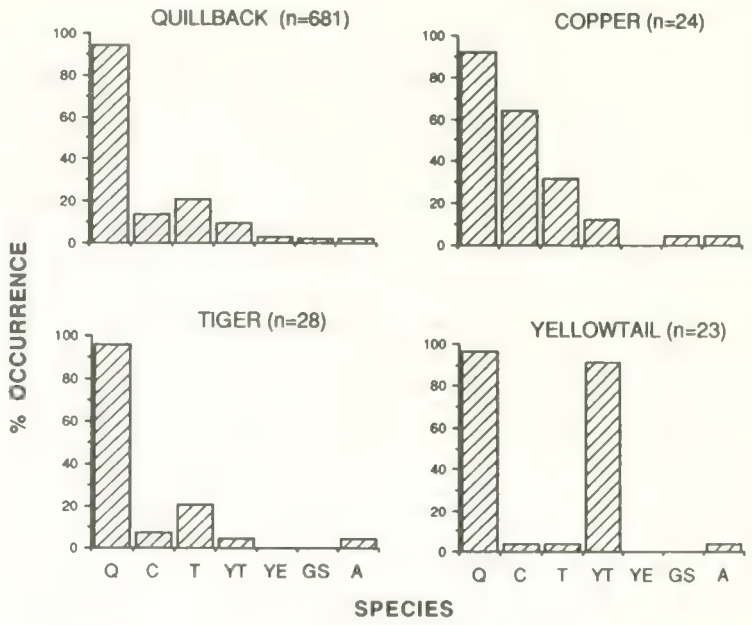

Figure 6

Percent occurrence of conspecific and heterospecific rockfish in association with quillback rockfish, *Sebastes maliger*; copper rockfish, *S. caurinus*; tiger rockfish, *S. nigrocinctus*; and yellowtail rockfish, *S. flavidus*; Species key: Quillback rockfish (Q), copper rockfish (C), tiger rockfish (T), yellowtail rockfish (YT), yelloweye rockfish (YE), greenstriped rockfish (GS), and alone (A).

Published information on in situ behavioral activity, species associations, and density of tiger rockfish is scarce, no doubt in part due to the consistently low densities in which this species is encountered. Tiger rockfish have been observed in low densities, and primarily as only a single fish encountered at any one time, in waters <30 m deep in Puget Sound (Moulton, 1977), in 21–140 m in the northeastern Strait of Georgia (Richards and Cass, 1985), in 64–305 m depths off Oregon (Pearcy et al., 1989), and in <30 m in Saanich Inlet (Murie, 1991). As 21% (6/28) of *S. nigrocinctus* were observed within 3 m of another tiger rockfish in our study (Fig. 6), this species may not be as 'solitary' as indicated by the previous studies. Density of tiger rockfish may be limited by the availability and defense of suitably large shelter holes, which the fish retreat into upon approach by a SCUBA diver (Murie, pers. obs.).

The depth distribution of rockfish in Saanich Inlet, and hence any size or species associations, may be influenced by a number of factors, including a) the physical regime of the inlet; b) the paucity of observations for relatively uncommon species; and c) the actual depth range and total number of transects surveyed with the submersible. The year-round oxygen deficiency in waters >100 m in Saanich Inlet, and the intermittent anoxia that occurs in waters of 125–234 m depth during January to August (Liu, 1989), may act to compress or shift the depth distribution of rockfish compared to open coastal waters where relatively deep water is not limiting in dissolved oxygen. In Saanich Inlet, squat lobsters, *Munida quadrispina*, migrate vertically en masse to avoid decreasing oxygen levels (Burd, 1983) although catastrophic mortality of spot prawns, *Pandalus platyceros*, in 85–90 m depth has been attributed to a sudden intrusion of displaced anoxic bottom-water into midwater depths (Jamieson and Pikitch, 1988). For mobile organisms (such as rockfish) decreasing oxygen levels may elicit a behavioral response involving a vertical or horizontal habitat shift (Kramer, 1987). Of three transects in Saanich Inlet that started at 150 m, no rockfish were observed at depths >115 m, and only three quillback rockfish were seen at depths >100 m (note: one of these transects was not used in the overall analysis owing to loss of the audio-track at <80 m). With the exception of copper rockfish, Hart (1973) reports maximum depths of >250 m for the other rockfish species. In addition, quillback, tiger, greenstriped, and yellowtail rockfish have been observed from submersibles at depths >120 m (Richards and Cass, 1985; Pearcy et al., 1989).

The scarcity of observations on relatively low density species of rockfish, especially in combination with time limitations of the submersible, could also affect our interpretation of rockfish depth distribution. In Saanich Inlet, few rockfish other than quill-

back rockfish were observed during the submersible dives. The depth range and density of the relatively uncommon species of rockfish may have been improved if we had been able to do more transects and, in the instance of maximum depths, by doing deeper transects. Bias in using submersible transects was exemplified by the downward bias (i.e. deeper) in the observed minimum depth ranges for tiger, yellowtail, and yelloweye rockfish in Saanich Inlet (Table 2). These rockfish species have been observed during SCUBA dives in Saanich Inlet in water as shallow as 15–25 m (Murie, pers. obs.). The density estimate and depth range for copper rockfish was probably also biased because of the reduced ability to maintain fine control of the *Pisces* buoyancy as it approaches shallower depths (~20 m). We know that copper rockfish in Saanich Inlet occur from near-surface waters (~2 m) and their distribution extends visibly below 40 m depth (Murie, 1991). The density of copper rockfish on rocky reefs in 20–30 m of water, however, can approach 50 fish·100m^{-2} (Murie, 1991), far in excess of any density observed for copper rockfish from the submersible (Table 2). In general, however, copper rockfish do occur in shallower water than quillback rockfish (Moulton, 1977; Richards, 1987; Murie, 1991), as was observed from the submersible transects in Saanich Inlet.

Another potentially important bias in the use of the *Pisces IV* to observe densities and activities of rockfish is whether the fish are attracted or noticeably repelled by the size, noise, and lights of the submersible. Similar to our study, Carlson and Straty (1981) noted that most of the rockfish were neither repelled nor attracted to the submersible while they observed them in southeastern Alaska. In addition, Richards (1986) observed that none of the common fish species seen in the northeastern Strait of Georgia seemed disturbed by the *Pisces IV* submersible. A notable exception in Carlson and Straty's (1981) study was large (7–10 kg) yelloweye rockfish that were obviously attracted to the submersible and actually followed it, similar to the ratfish and sixgill shark in our study. Pearcy et al. (1989) also noted that large schools of yellowtail rockfish were attracted to their submersible and followed it over substantial periods of time and depth; there was no visible evidence, however, of schools of yellowtail rockfish following the *Pisces* in our study.

The occurrence of perching and hovering activities observed for the majority of rockfish in Saanich Inlet from the *Pisces* was consistent with behavioral activities of quillback and copper rockfish observed with SCUBA in Saanich Inlet (Murie, 1991). Observations from the submersible were limited in this respect because it was impossible to look into all crevices or into shelter holes under rocks for the presence of fish. Tiger and yelloweye rockfish could be seen in shelter holes and crevices but their size could not always be estimated. Although the *Pisces* approaches shelter holes from below (during its ascent), fish in deep shelter holes and crevices may not be detected. The presence of fish in crevices and shelter holes was therefore probably underestimated. Nevertheless, at present, submersibles and remotely-operated vehicles (ROVs) provide the best means of observing the activities of rockfish occupying complex habitat in deep water.

Although it is evident from submersible observations that estimates of abundance and activities of rockfish involve a variety of biases, these direct visual assessments can provide quantitative information on the densities and depth distributions of rockfish species in habitats that cannot be surveyed adequately using bottom trawls. In addition, submersibles allow direct observation of the behavioral activities and associations of individual fish in relation to specific habitat types. This type of information has not been attainable using conventional survey techniques of fisheries.

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Literature cited

Anderson, J. J., and A. H. Devol.
1973. Deep water renewal in Saanich Inlet, an intermittently anoxic basin. Estuarine and Coastal Mar. Sci. 1:1–10.

Boehlert, G. W.
1980. Size composition, age composition, and growth of canary rockfish, *Sebastes pinniger*, and splitnose rockfish, *S. diploproa*, from the 1977 rockfish survey. Mar. Fish. Rev. 42: 57–63.

Burd, B. J.
1983. The distribution, respiration and gills of a low oxygen tolerant crab, *Munida quadrispina* (Benedict, 1902) (Galatheidae, Decapoda) in an intermittently anoxic fjord. M.Sc. thesis, Biology Dept. Univ. Victoria, Victoria, B.C., 151 p.

Carlson, H. R., and R. R. Straty.
1981. Habitat and nursery grounds of Pacific rockfish, *Sebastes* spp., in rocky coastal areas of southeastern Alaska. Mar. Fish. Rev. 43:13–19.

Dennis, G. D., and T. J. Bright.
1988. Reef fish assemblages on hard banks in the northwestern Gulf of Mexico. Bull. Mar. Sci. 43:280–307.

Hallacher, L. E., and D. A. Roberts.
1985. Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay, California. Env. Biol. Fish. 12:91–110.

Hart, J.
1973. Pacific fishes of Canada. Fish. Res. Board Can. Bull. 180:407–443.

Herlinveaux, R.
1962. Oceanography of Saanich Inlet in Vancouver Island, British Columbia. J. Fish. Res. Board Can. 19:1–37.

Jamieson, G. S., and E. K. Pikitch.
1988. Vertical distribution and mass mortality of prawns, *Pandalus platyceros*, in Saanich Inlet, British Columbia. Fish. Bull. 86:601–608.

Kramer, D. L.
1987. Dissolved oxygen and fish behavior. Env. Biol. Fish. 18:81–92.

Krieger, K.
1993. Distribution and abundance of rockfish determined from a submersible and by bottom trawling. Fish. Bull. 91:87–96.

Larson, R. J.
1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecol. Monogr. 50: 221–239.

Liu, Q.
1989. Ecophysiological studies of *Orchomenopsis affinis* (Holmes) (Lysianassidae, Amphipoda) in an intermittently anoxic fjord. M.Sc. thesis, Biology Dept., Univ. Victoria, Victoria, B.C., 122 p.

Mackie, G. O., and C. E. Mills.
1983. Use of the *Pisces IV* submersible for zooplankton studies in coastal waters of British Columbia. Can. J. Fish. Aquat. Sci. 40:763–776.

Martin, D. W., P. A. Mayes, and V. W. Rodwell.
1981. Harper's review of biochemistry, 18th ed. Lange Medical Pub., Los Altos, CA, 126 p.

Mathews, S. B., and M. W. Barker.
1983. Movements of rockfish (*Sebastes*) tagged in northern Puget Sound. Fish. Bull. 82: 916–922.

Matthews, K. R.
1990. A comparative study of habitat use by young-of-the-year, subadult, and adult rockfishes on four habitat types in central Puget Sound. Fish Bull. 88:223–239.

Moulton, L.
1977. An ecological analysis of fishes inhabiting the rocky nearshore regions of northern Puget Sound, Washington. Ph.D. diss., Univ. Washington, Seattle, WA, 181 p.

Murie, D. J.
1991. Comparative ecology and interspecific competition between the sympatric congeners *Sebastes caurinus* (copper rockfish) and *S. maliger* (quillback rockfish). Ph.D. diss., Univ. Victoria, Victoria, B.C., 287 p.

Patten, B. G.
1973. Biological information on copper rockfish in Puget Sound, Washington. Trans. Am. Fish. Soc. 102:412–416.

Pearcy, W. G., D. L. Stein, M. A. Hixon, E. K. Pikitch, W. H. Barss, and R. M. Starr.
1989. Submersible observations of deep-reef fishes of Heceta Bank, Oregon. Fish. Bull. 87:955–965.

Pickard, G. L.
1963. Oceanographic characteristics of inlets of Vancouver Island, British Columbia. J. Fish. Res. Board Can. 20:1109–1144.

Richards, L. J.
1986. Depth and habitat distributions of three species of rockfish (*Sebastes*) in British Columbia: observations from the submersible *Pisces IV*. Env. Biol. Fish. 17:13–21.
1987. Copper rockfish (*Sebastes caurinus*) and quillback rockfish (*Sebastes maliger*) habitat in the Strait of Georgia, British Columbia. Can. J. Zool. 65:3188–3191.

Richards, L. J., and A. J. Cass.
1985. Transect counts of rockfish in the Strait of Georgia from the submersible *Pisces IV*, October and November 1984. Can. Fish. Aquat. Sci. Data Rep. No. 511, 99 p.

Richards, L. J., C. M. Hand, and J. R. Candy.
1988. 1988 research catch and effort data on nearshore reef-fishes in British Columbia statistical areas 12 and 13. Can. Fish. Aquat. Sci. Man. Rep. No. 2000, 89 p.

SAS (SAS Institute Inc.).
1985. SAS User's guide: statistics, vers. 5. Cary, NC, 956 p.

Stein, D. L., B. N. Tissot, M. A. Hixon, and W. Barss.
1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. Fish. Bull. 90:540–551.

Thomson, R. E.
1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56, 291 p.

Uzmann, J. R., R. A. Cooper, R. B. Theroux, and R. L. Wigley.
1977. Synoptic comparison of three sampling techniques for estimating abundance and distribution of selected megafauna: submersible vs. camera sled vs. otter trawl. Mar. Fish. Rev. 39:11–19.

Westrheim, S.J.
1970. Survey of rockfishes, especially Pacific ocean perch, in the northeastern Pacific Ocean, 1963–66. J. Fish. Res. Board Can. 27:1781–1809.

Wilkins, M.E.
1980. Size composition, age composition, and growth of chilipepper, *Sebastes goodei,* and bocaccio, *S. paucispinis,* from the 1977 rockfish survey. Mar. Fish. Rev. 42:48-53.

Reexamination of geographic variation in cranial morphology of the pantropical spotted dolphin, *Stenella attenuata*, in the eastern Pacific

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Abstract.—The spotted dolphin (*Stenella attenuata*) is found throughout much of the eastern tropical Pacific Ocean. A previous study evaluated morphological variation in skull morphology, but now specimens are available for a greater portion of the range. Also, corrections have been made in data and an assessment has been made evaluating repeatability of character measurements. We reassessed geographic variation in 30 cranial features (26 morphometric measures and 4 tooth counts) based on 611 museum specimens. All characters except two tooth counts showed statistically significant geographic variation, while 21 of the 30 characters exhibited significant sexual dimorphism. Males were larger in most characters; females were larger in some length measurements involving the rostrum and ramus. As in previous analyses, inshore *S. attenuata* were found to be very distinctive, so subsequent analyses focused on offshore spotted dolphins from 29 5° latitude-longitude blocks. Mantel tests and matrix correlations for 19 of the 30 features demonstrated significant "regional patterning," whereas 22 of the characters were shown to have "local patterning." Principal-components, canonical-variates, and cluster (UPGMA and function-point) analyses also were employed to assess geographic variation. In the eastern portion of the range, the subdivision between northern and southern offshore *S. attenuata* found in the previous investigation was confirmed. In general, blocks to the west (including one encompassing part of the Hawaiian Islands) were more like the southern blocks than those of the northeast. Morphological patterns were similar to those found in a number of environmental variables, particularly water depth, solar insolation (January), sea surface temperature (January and July), surface salinity, and thermocline depth (winter and summer). Present management units are inconsistent with the pattern of cranial variation; spotted dolphins from west of lat. 120°W probably should not be pooled with those to the east, as they show closer affinity with the Southern Offshore unit. In addition, the boundary between the Northern and Southern units should probably be moved north to about lat. 5°N.

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Spinner and spotted dolphins (*Stenella longirostris* and *S. attenuata*) have broadly overlapping ranges in the eastern tropical Pacific Ocean (Perrin et al., 1983). Information concerning geographic variation of these species is of both intrinsic scientific and practical interest. Dolphins in the region are killed as a result of purse-seining for yellowfin tuna (*Thunnus albacares*; Allen, 1985). The tuna often are found in association with these two dolphin species (or with *Delphinus delphis*), and fishermen set nets on the dolphin schools to capture tuna found below the dolphins. Estimates indicate that from 1985 to 1990 roughly 53,000 to 129,000 dolphins were killed annually as a result of fishing operations (Hall and Boyer 1987, 1988, 1989, 1990, 1991, 1992). Most recently the annual kill has dropped to approximately 15,000 to 27,000 (Hall and Lennert[1,2]). Government regulations in the United States set limitations on U.S. vessels with respect to the extent of dolphin mortality that will be permitted. Dolphins are managed by defining a series of management stocks. Data, such as those on skull morphology, can provide insight into the underlying population subdivision and may be of considerable value in defining geographic boundaries of biologically relevant management stocks (Dizon et al., 1992).

Douglas et al. (1992) have provided a detailed assessment of geographic variation in cranial morphology of spinner dolphins. For spotted dolphins, the most recent geographic-variation analyses using skull characteristics were by Douglas et al. (1984) and Schnell et

[1] Hall, M. A., and C. Lennert. 1992. Estimates of incidental mortality of dolphins in the purse-seine fishery for tunas in the eastern Pacific Ocean in 1991. Int. Whal. Commn. meeting doc. SC/44/SM6, 5 p.

[2] Hall, M. A., and C. Lennert. 1993 Incidental mortality of dolphins in the eastern Pacific Ocean tuna fishery in 1992. Int. Whal. Commn. meeting doc. SC/45/SM1, 5 p.

al. (1986). Numerous additional specimens have become available, particularly from the western portion of the range and Hawaii. The repeatability of 36 skull measures used in previous studies (Douglas et al., 1984; Schnell et al., 1986) was appraised, as was done previously by Douglas et al. (1992) for spinner dolphins. Also, some immature specimens had inadvertently been incorporated into the previous spotted dolphin analyses. For these reasons, we have undertaken a reassessment of geographic variation and sexual dimorphism of spotted dolphins from the eastern tropical Pacific. This study provides an opportunity to re-evaluate variation patterns previously described and to compare directly patterns of variation found in spotted and spinner dolphins.

Materials and methods

Overall, data-gathering and assessment procedures outlined by Douglas et al. (1992) were used. We measured 611 adult museum specimens (maturity evaluated on the basis of premaxilla fusion with maxilla at distal end of rostrum; Dailey and Perrin, 1973) of spotted dolphins (Fig. 1). These included 534 of 613 specimens used in earlier studies (Douglas et al., 1984; Schnell et al., 1986; 79 specimens previously used had been incorrectly aged or had inadequate locality data) along with 77 new specimens.

As was done with spinner dolphins (Douglas et al., 1992), the first specimen set was measured by M. E. Douglas and the new specimens by W. F. Perrin. In addition, Perrin remeasured 81 specimens of spinner and spotted dolphins measured by Douglas to determine whether measurements were repeatable. Initially, 36 characters were evaluated (illustrations and character definitions given in Schnell et al., 1985). Comparisons of measurements taken on the same specimens by the two investigators indicated that 6 of the original 36 measurements (i.e. width of left premaxillary [at midline of nares], width of right premaxillary [at midline of nares], separation of pterygoids, length of left tympanic cavity, length of right tympanic cavity, and width at pterygobasioocipital sutures) should be deleted, because we were not able consistently to repeat these measurements. For some other measurements, there were differences between investigators, but the differences were consistent (e.g. one obtained measurements that were smaller than those reported by the other). Therefore, we calculated regression equations for each of the remaining characters based on the 81 jointly measured specimens. These regression equations were used to convert the measurements from the rest of the initial specimens to appropriate values for inclusion with the measurements taken by Perrin. Through these procedures, we developed a data set of 30 characters (see Table 1) for the 611 specimens.

Specimens were not used if, because of damaged parts, we could not obtain most of the 30 measurements. Missing values (0.50% of total) for included specimens were estimated by linear regression[3] onto the character that explained the greatest proportion of the variance for the variable being considered.

Animals were assigned to 5° latitude-longitude blocks and each geographic block assigned a numerical code (see Fig. 1). These codes were modified slightly from those employed by Schnell et al. (1986) to accommodate new specimens from more westerly blocks. We had specimens available from 41 blocks, 8 of which were represented by only a single specimen and 4 of which were inshore blocks (i.e. contained only specimens of the inshore form; Douglas et al., 1984). The 29 blocks that were not inshore blocks and had more than one specimen were used as the basis for most geographic variation analyses. While several of the 29 blocks have relatively small samples, geographic-patterning tests (described below) suggested that, in general, sample values are representative of what is expected for these blocks based on their geographic positions.

Schnell et al. (1985) showed *S. attenuata* to be sexually dimorphic for 23 of 36 characters. Because some specimens used in that analysis were removed and new specimens added (see above), we conducted a two-way analysis of variance (ANOVA) for block and sex, based on specimens in the 11 blocks with at least four of each sex (Fig. 1). Correction terms were obtained to adjust measurements of the larger sex downward and the smaller sex upward, thus producing sex-adjusted or "zwitter" measurements (method described in more detail by Schnell et al., 1985). As a result, we were able to combine specimens for both sexes in an overall analysis of geographic variation.

To assess whether combining specimens from different cruise sets within blocks confounded geographic patterns based on blocks, we performed a nested ANOVA for cruise sets within the 12 blocks for which two specimens were obtained from at least two cruise sets. Blocks employed in this analysis (with numbers of cruise sets in parentheses) were the following: 0215 (4), 0216 (3), 0312 (2), 0506 (2), 0507 (2), 0512 (9), 0513 (10), 0515 (2), 0612(6), 0613 (7), 0615 (3), and 0712 (2).

[3] "Missing Data Estimator" program by Dennis M. Power, Santa Barbara Mus. Nat. Hist., pers. commun. 1975.

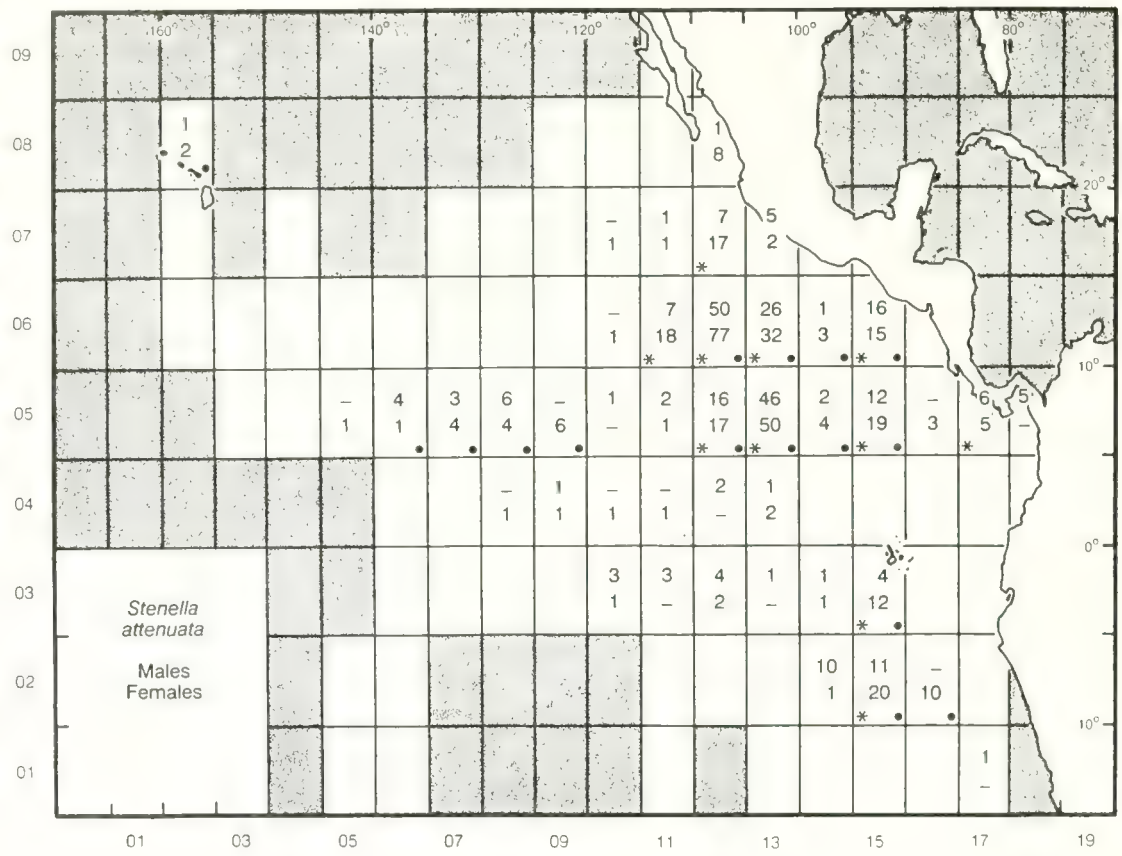

Figure 1

Known range of *Stenella attenuata* in eastern tropical Pacific Ocean (based on Perrin et al., 1983), with numbers of males (above) and females (below) available for each 5° latitude-longitude block (total of 611 specimens). Each block is identified by numerical code (numbers on left and bottom margins are combined; e.g. block 0802 encompasses the northern Hawaiian Islands). Asterisks indicate the 11 blocks included in analysis of sexual dimorphism. Initial analyses indicated that specimens in four blocks (0516, 0517, 0518, 0812) represented a well differentiated inshore form (see Douglas et al., 1984); thus, these were not used in subsequent evaluations. The remaining 29 blocks with two or more specimens were used as the basis for analyses of geographic variation; for some evaluations, the eight blocks with single specimens were projected onto axes based on the other 29 blocks. For the 16 blocks marked with a dot in lower-right corner, sufficient numbers of *S. attenuata* and *S. longirostris* (i.e. at least two of each species) were available for interspecific comparison of geographic trends.

Correlation, ordination, and clustering

After conversion to zwitters, characters were standardized (means=0, standard deviations=1). Product-moment correlations were computed among characters, and associations among characters were summarized by clustering characters (unweighted pair-group method with arithmetic averages; UPGMA). This technique is a type of hierarchical cluster analysis that also was used to summarize average distance coefficients (Sneath and Sokal, 1973) calculated for all pairs of blocks based on standardized data. Cophenetic correlation coefficients indicate the extent to which distances in resulting dendrograms accurately represented original interblock morphologic distances.

Standardized data also were summarized by using a nonhierarchical K-group method (function-point cluster analysis; described in Katz and Rohlf [1973] and Rohlf et al. [1979]). Through use of this technique, blocks are assigned to subgroups at a specified level. A w-parameter value used in function-point clustering was varied. An hierarchical, but not necessarily nonoverlapping, system of clusters was

Table 1

Geographic variation and sexual dimorphism in *Stenella attenuata* evaluated for 30 characters.

Character[1]	*F*–value[2]		Mean[3]		Correction factor[4]	Percentage difference[5]
	Block	Sex	Male	Female		
1 Condylobasal L.	10.59***	1.94	397.0	398.2	–0.74	–0.30
2 L. Rostrum (from Base)	6.94***	13.49***	236.7	239.5	–1.55	–1.20
3 L. Rostrum (from Pterygoid)	6.88***	6.84**	278.5	281.0	–1.31	–0.87
4 W. Rostrum (at Base)	14.20***	25.13***	83.3	81.8	0.73	1.85
5 W. Rostrum (at 1/4 L.)	12.25***	51.82***	57.1	55.2	0.90	3.32
6 W. Rostrum (at 1/2 L.)	13.82***	47.61***	42.4	40.9	0.78	3.78
7 W. Premax. (at 1/2 L.)	8.51***	72.88***	23.6	22.4	0.60	5.25
8 W. Rostrum (at 3/4 L.)	8.65***	73.90***	29.9	28.0	0.96	6.66
9 Preorbital W.	16.92***	45.92***	149.5	146.6	1.43	1.97
10 Postorbital W.	22.46***	42.23***	167.8	165.1	1.31	1.63
11 Skull W. (at Zygomatic P.)	21.98***	51.05***	167.4	164.5	1.46	1.79
12 Skull W. (at Parietals)	5.73***	54.11***	129.6	136.4	1.58	2.34
13 Ht. Braincase	10.61***	53.87***	95.9	93.7	1.04	2.36
14 L. Braincase	15.67***	39.94***	113.1	111.2	0.95	1.71
15 Max. W. Premax.	8.89***	4.45*	66.2	65.7	0.27	0.85
16 W. External Nares	7.38***	0.03	42.5	42.5	0.01	0.02
17 L. Temporal Fossa	22.41***	16.79***	70.1	68.4	0.82	2.53
18 W. Temporal Fossa	20.60***	28.50***	55.2	53.2	0.93	3.72
19 Orbital L.	2.97**	0.06	47.4	47.4	0.02	0.10
20 L. Antorbital P.	8.33***	4.30*	36.9	36.4	0.24	1.43
21 W. Internal Nares	9.58***	12.80***	47.4	46.6	0.36	1.58
22 L. Up. Toothrow	6.20***	10.56**	204.3	206.7	–1.29	–1.16
23 No. Teeth (Up. Lf.)	0.96	1.54	41.4	41.2	0.10	0.47
24 No. Teeth (Up. Rt.)	0.98	0.65	41.3	41.1	0.07	0.33
25 No. Teeth (Low. Lf.)	2.89*	0.02	41.0	40.9	–0.01	–0.02
26 No. Teeth (Low. Rt.)	2.82**	1.02	40.8	41.0	–0.08	–0.36
27 L. Low. Toothrow	5.38***	11.63***	198.6	201.2	–1.40	–1.28
28 Ht. Ramus	16.13***	0.12	57.3	57.1	0.38	0.24
29 Tooth W.	12.14***	19.65***	3.4	3.3	0.06	3.55
30 L. Ramus	9.02***	8.86**	335.5	338.3	–1.48	–0.82

[1] Abbreviations: Ht. = height; L. = length; Lf. = left; Low. = lower; Max. = maximum; No. = number; P. = process; Premax. = premaxillary; Rt. = right; Up. = upper; W. = width.
[2] *F*-values from main effects two-way analysis of variance (5° block vs. sex) involving 11 blocks (*P< 0.05; **P< 0.01; ***P< 0.001). Total of 170 individuals. Degrees of freedom 10 for among-block variation and 1 for between sexes.
[3] Unweighted mean for 11 blocks.
[4] Added to all individual female measurements and subtracted from all individual male measurements to correct for sexual differences.
[5] Difference between sexes (males minus females) multiplied by 100; the resulting value was divided by average of male and female means.

obtained by repeating the analysis at different clustering levels. Results are displayed in modified skyline diagrams (Wirth et al., 1966).

Using standardized data, we constructed scatter diagrams by projecting blocks onto the first two principal components (Sneath and Sokal, 1973) extracted from a matrix of correlations among the 30 characters. Canonical-variates analysis also was employed to obtain the subset of variables that shows the greatest interblock separation relative to intrablock variation (Program P7M of BMDP statistical software; Dixon, 1990). Plots of the first two canonical variables show the maximum separation of blocks in two-dimensional space.

Mantel test for geographic patterning

A Mantel (1967) test was used to assess interlocality variation in each character and determine whether measures are geographically patterned or, alterna-

tively, vary spatially at random. The observed association between sets of character differences and geographic distances was tested relative to its permutational variance, and the resulting statistic compared against a Student's t-distribution with infinite degrees of freedom. We performed analyses using GEOVAR, a computer-program library for geographic variation analysis (written by David M. Mallis and provided by Robert R. Sokal, State University of New York at Stony Brook).

Character differences were compared first with actual geographic distances (in nautical miles) between centers of blocks and then with reciprocals of distances. In evaluations of reciprocals, where distances are scaled in a nonlinear manner, longer distances are considered effectively to be equal, and the portion of the scale involving smaller distances is expanded. Thus, use of reciprocals of distances increases the power of analyses to reveal geographic patterns that are "local" in nature (i.e. involving closely placed blocks), whereas tests involving nautical-mile distances evaluate "regional" trends. Positive associations of character differences and nautical-mile distances are indicated by positive t-values, while negative t-values denote such associations when using distance reciprocals. Douglas et al. (1992) provided a simplified example to demonstrate use of the Mantel procedure.

We also computed matrix correlations (Sneath and Sokal, 1973) between character differences and the associated geographic distances or reciprocals of distances between localities. The statistical significance of these coefficients cannot be tested in the conventional way, because all pairs of localities were used and these are not statistically independent. However, the resulting values can be used as descriptive statistics indicating the degree of association of difference values.

Morphological-environmental covariation

We calculated product-moment correlations of block means for morphological characters with environmental variables. Data were available for 13 environmental variables for the eastern tropical Pacific Ocean (Table 2; data sources summarized in Douglas et al., 1992). The list of environmental variables used is somewhat different than that employed by Schnell et al. (1986), because data for some of the variables were not available for all blocks in the broader geographic range being considered in the current study. We also used UPGMA to summarize associations among these environmental variables for 51 blocks; since these two dolphin species have broadly overlapping distributions in the eastern tropical Pacific, the blocks used are representative of areas inhabited by *S. attenuata*.

In order to obtain summary variables reflecting overall environmental trends, we conducted a principal-components analysis of the 13 environmental variables for 51 blocks with specimens of *S. longirostris* (Douglas et al., 1992) or *S. attenuata* or both. Individual blocks were projected onto the resulting environmental principal components based

Table 2

Environmental measurements compiled for each 5° latitude-longitude block.[1]

1 Sea Current (N., Winter)—Average northern component (in knots) of surface water current in winter.

2 Sea Current (W., Winter)—Average western component (in knots) of surface water current in winter.

3 Water Depth—Average sea depth (in m).

4 Solar Insolation (Jan.)—Average incoming solar radiation for January (in gm·cal/cm^2).

5 Solar Insolation (Annual)—Average annual incoming solar radiation in gm·cal/cm^2).

6 Sea Surface Temp. (Jan.)—Average January sea surface temperature (in°C).

7 Sea Surface Temp. (July)—Average July sea surface temperature (in°C).

8 Sea Surface Temp. (Ann. Var.)—Average annual sea surface temperature variation (in°C).

9 Oxygen Min. Layer (Depth)—Annual mean depth (in m) of absolute oxygen minimum surface with respect to the vertical.

10 Surface Salinity—Average salinity (‰) of surface sea water.

11 Thermocline Depth (Winter)—Mean depths (in m) to top of thermocline for January, February, and March.

12 Thermocline Depth (Summer)—Mean depths (in m) to top of thermocline for July, August, and September.

13 Surface Dissolved Oxygen—Annual mean dissolved oxygen (mL/L) of surface sea water.

[1] Data sources listed in Douglas et al. (1992: table 2). Abbreviations: Ann. Var. = annual variation; Jan. = January; Min. = minimum; N. = north; Temp. = temperature; W. = west.

on standardized data. These environmental components served as composite environmental variables for comparisons with morphological variables.

Matrix correlations and Mantel tests were used to test for local and regional patterning of environmental variables. Also, differences between each pair of blocks for a given morphological variable were compared with those for an environmental variable.

Interspecific comparisons

The predominant trends in the data sets for each of *S. attenuata* and *S. longirostris* were summarized with principal components and canonical variables. Information is available for 16 blocks from which both offshore *S. attenuata* and *S. longirostris* were sampled (Fig. 1). These blocks are representative of the total geographic range investigated in our studies. In order to compare general patterns of variation in the two species, we calculated product-moment correlations, Mantel tests, and matrix correlations for individual morphological characters, principal-component projections, and canonical-variable projections of these 16 blocks.

In our analyses, average distances based on morphological characters were computed between each pair of localities. To evaluate the extent of similarity in geographic patterns, the original distance matrices for each species were modified such that only distances among the 16 localities common to both species were included. These matrices were then compared by using the Mantel test and computing the matrix correlation.

Results

Sexual dimorphism

Table 1 includes mean measurements for males and females based on 11 blocks. For two-way ANOVAs assessing geographic block and sex (df=21, n=461), all but 5 of the 30 were very highly significant (P<0.001). The probability was 0.02 for number of teeth (lower right) and 0.007 for orbital length. Two characters showed no significant variation (upper tooth counts) and one character (number of teeth [lower left]) was close to significant (P<0.06). Statistically significant interactions (P<0.05) between block and sex were found for five of the characters: condylobasal length; width of rostrum (at 1/4 length); width of rostrum (at 1/2 length); width of rostrum (at 3/4 length); and width of internal nares. Interaction denotes that the degree of sexual dimorphism differs among blocks for these characters.

Sexual dimorphism was significant for 22 of the 30 characters (Table 1). Females had longer rostrums, which is reflected in a number of characters (i.e. 2, 3, 22, 27, 30). In general, males had wider skulls and tended to be larger for nonrostral portions of the skull. Percentage differences between sexes are presented in Table 1. The average absolute difference (i.e. sign ignored) between the sexes for the 30 characters was 1.78%. For 8 characters where females were larger, the average difference was 0.75%, whereas for 22 characters where males were larger the average difference was 2.16%. The greatest differences were found for width of premaxillary (at 1/2 length) and width of rostrum (at 3/4 length)—5.25% and 6.66%, respectively.

Table 3 shows the results for the nested ANOVA for cruise sets within blocks. Twenty-three of the 30 characters showed highly significant or very highly significant block effects, whereas only three characters (those involving the temporal fossa and length of braincase) reflected highly significant or very highly significant effects for cruise set. Even in those three cases, block effects were more pronounced. Therefore, we conclude that combining cruise sets into blocks did not have an important confounding influence on geographic patterns found among blocks.

Correlation, ordination, and clustering

Most character pairs had positive correlations. An exception was tooth counts and temporal fossa measurements, which tended to have negative correlations with skull width measurements. The dendrogram in Figure 2 summarizes absolute correlations (i.e. sign of correlation ignored) among characters based on 29 blocks to provide an assessment of character covariation. The width of external nares was the character with the least association with other measures. Tooth characters join and are separated from the remaining morphometric characters. Braincase measures and skull width (at parietals) cluster in another relatively distinct group. The remaining characters are arranged in two groups. The cluster at the top of Figure 2 includes most length measurements and height of ramus. Width measurements along with length of antorbital process, orbital length, and length of temporal fossa are included in the adjoining major cluster (Fig. 2).

Table 4 includes character loadings on the first two principal components based on data for 29 blocks. Component I explains 45.0% of the total variance for the 30 characters, whereas component II summarizes an additional 16.8% (cumulative total of 61.8%). Projections of blocks onto the two components are depicted in Figure 3, and a map (Fig. 4) is included that renders geographic block projections onto the first component. Component I repre-

Table 3

Results of nested ANOVA (F-values) for different cruise sets within 12 latitude-longitude blocks of offshore *Stenella attenuata*.

	F–value	
Character[1]	Cruise set	Block
1 Condylobasal L.	1.28	3.03***
2 L. Rostrum (from Base)	1.34	3.25***
3 L. Rostrum (from Pterygoid)	1.65*	4.36***
4 W. Rostrum (at Base)	1.25	8.86***
5 W. Rostrum (at 1/4 L.)	1.60*	7.51***
6 W. Rostrum (at 1/2 L.)	1.12	8.34***
7 W. Premax. (at 1/2 L.)	1.29	5.25***
8 W. Rostrum (at 3/4 L.)	1.01	5.39***
9 Preorbital W.	1.25	10.87***
10 Postorbital W.	1.22	11.31***
11 Skull W. (at Zygomatic P.)	1.27	10.81***
12 Skull W. (at Parietals)	0.97	1.11
13 Ht. Braincase	1.55*	1.55
14 L. Braincase	1.83**	3.59***
15 Max. W. Premax.	1.22	4.01***
16 W. External Nares	0.95	3.00***
17 L. Temporal Fossa	2.13***	7.54***
18 W. Temporal Fossa	1.87**	9.48***
19 Orbital L.	1.29	1.24
20 L. Antorbital P.	0.82	5.00***
21 W. Internal Nares	1.09	3.47***
22 L. Up. Toothrow	1.33	2.67**
23 No. Teeth (Up. Lf.)	1.23	1.22
24 No. Teeth (Up. Rt.)	1.19	0.78
25 No. Teeth (Low. Lf.)	1.47*	2.57**
26 No. Teeth (Low. Rt.)	1.45*	2.57**
27 L. Low. Toothrow	1.63*	2.45**
28 Ht. Ramus	1.09	1.77
29 Tooth W.	1.31	1.45
30 L. Ramus	1.25	2.37**

* $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$
Abbreviations identified in Footnote 1 of Table 1

Table 4

Principal component loadings for offshore *Stenella attenuata* involving character means for 29 latitude-longitude blocks.

	Component[2]	
Character[1]	I	II
1 Condylobasal L.	**0.812**	–0.505
2 L. Rostrum (from Base)	0.786	–0.483
3 L. Rostrum (from Pterygoid)	0.795	–0.446
4 W. Rostrum (at Base)	**0.867**	0.206
5 W. Rostrum (at 1/4 L.)	**0.923**	0.157
6 W. Rostrum (at 1/2 L.)	**0.855**	0.308
7 W. Premax. (at 1/2 L.)	**0.863**	0.161
8 W. Rostrum (at 3/4 L.)	**0.868**	0.211
9 Preorbital W.	**0.930**	0.235
10 Postorbital W.	**0.940**	0.181
11 Skull W. (at Zygomatic P.)	**0.938**	0.173
12 Skull W. (at Parietals)	0.740	0.270
13 Ht. Braincase	–0.002	0.225
14 L. Braincase	0.508	–0.325
15 Max. W. Premax.	0.366	–0.059
16 W. External Nares	0.286	–0.311
17 L. Temporal Fossa	–0.544	–0.576
18 W. Temporal Fossa	–0.375	–0.541
19 Orbital L.	0.655	–0.018
20 L. Antorbital P.	**0.805**	0.203
21 W. Internal Nares	0.604	0.000
22 L. Up. Toothrow	0.705	–0.588
23 No. Teeth (Up. Lf.)	–0.137	**–0.668**
24 No. Teeth (Up. Rt.)	–0.112	**–0.726**
25 No. Teeth (Low. Lf.)	–0.301	**–0.673**
26 No. Teeth (Low. Rt.)	–0.341	**–0.635**
27 L. Low. Toothrow	0.680	**–0.632**
28 Ht. Ramus	0.608	0.355
29 Tooth W.	–0.129	0.118
30 L. Ramus	**0.803**	–0.528

[1] Abbreviations identified in Footnote 1 of Table 1.
[2] Relatively high loadings highlighted in bold as follows (component I: > |0.81|, component II: > |0.61|).

sents general size, with relatively high character loadings (Table 4) for most characters, the exceptions being tooth characters and the two measurements of the temporal fossa. The specimens from blocks in the northeastern portion of the range tend to be small (Figs. 3 and 4), whereas those to the south and southwest typically are larger. The largest specimens were found in block 0802, which encompasses a portion of the Hawaiian Islands. Component II reflects tooth counts and measurements associated with toothrow length (Table 4). Blocks with relatively high values for these characters are found near the top of Figure 3, whereas those with low values tend to be near the bottom.

Blocks with single specimens were not used in the delineation of the principal components but have been projected onto components calculated by using the 29 blocks (Fig. 3). In general, the single-specimen blocks fall close to where one would predict based on their geographic position; some exceptions are expected based simply on expected chance variation.

Interblock morphological differences are summarized in the phenogram in Figure 5. Two blocks (0312 and 0802) are loosely joined in the most disparate cluster. Remaining blocks are divided into two clusters. The one represented at the top of Figure 3 includes the blocks from the south, southwest, and west, whereas the other includes blocks from the northeastern portion of the range.

Clusters based on the function-point procedure are summarized in the modified skyline diagram in Figure 6A. The most distinctive block is 0802 (en-

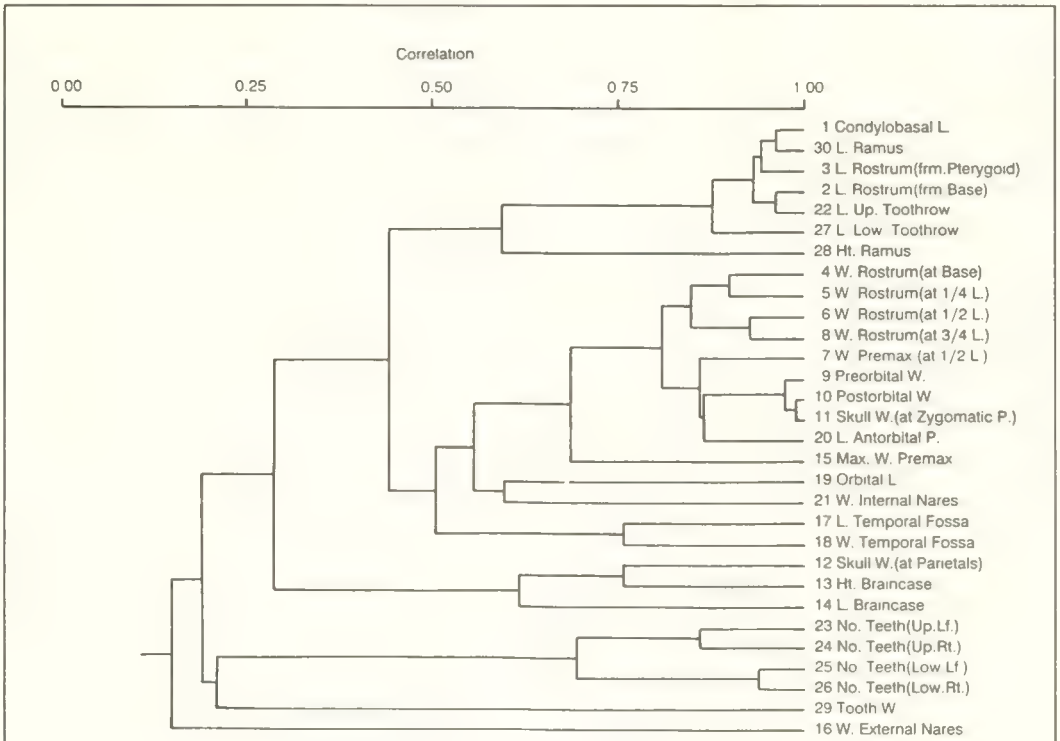

Figure 2

Correlations among characters based on character means for 29 latitude-longitude blocks. Clustering performed using UPGMA on absolute correlations among characters (i.e. negative signs removed). Cophenetic correlation coefficient is 0.87.

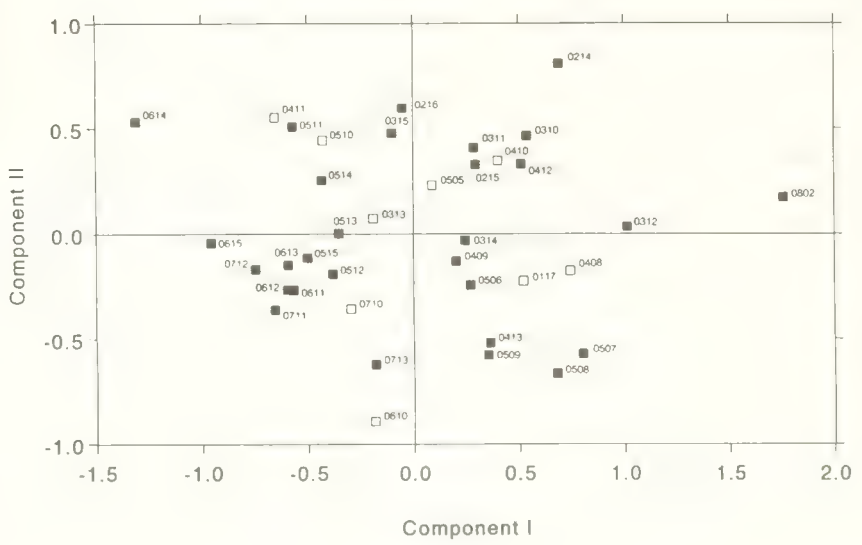

Figure 3

Projections of blocks onto first two principal components based on 30 characters. Solid symbols indicate 29 latitude-longitude blocks on which analysis was conducted. Open symbols represent blocks with only single specimens projected onto axes generated from 29 blocks with two or more specimens.

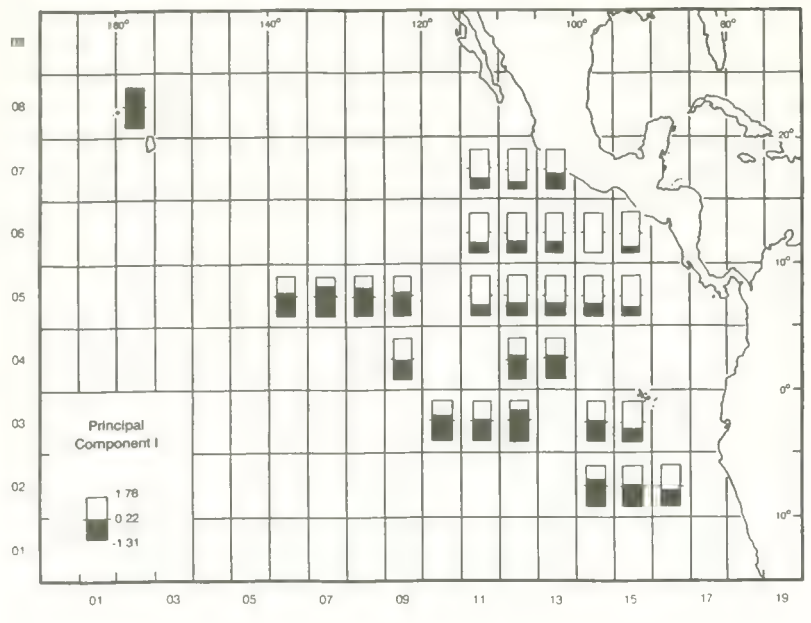

Figure 4

Geographic variation in principal component I. Bar represents range (low to high block values), and midpoint is marked. Darkened part of bar indicates value for particular latitude-longitude block.

compassing part of Hawaiian Islands) at the right of the diagram. A number of single blocks (0312, 0314, 0311) are separated from the others at w-values of 3.10 and 2.87. Most of the blocks from the northeastern portion of the range were included in a single cluster at lower w-values, although some individual blocks were separated by themselves (e.g. 0614, 0711).

In Figure 6B, a skyline diagram is included that is based on five characters: length of rostrum (from pterygoid); preorbital width; length of braincase; length of temporal fossa; and width of temporal fossa. These variables were identified by using canonical-variates analysis (reported below) as those that in combination provided the greatest discrimination among blocks. The use of function-point clustering on these selected characters provided clusters that persisted through several clustering levels. At the w-value of 1.38, four clusters were formed. The Hawaiian Island block (0802) is in a group by itself (on left side of Fig. 6B). The blocks to the south, southwest, and west are in a second assemblage (i.e. 0214 through 0506), while the northeastern blocks form the other major cluster (i.e. 0513 through 0713). Block 0711 is separated into its own group. At w-values less than 1.38, the second cluster is subdivided and the southern blocks are included with some from the southwest.

Canonical-variates analysis selected five characters (Table 5). Blocks are projected onto the first two canonical variables resulting from this analysis (Fig. 7), whereas Figure 8B shows geographically the distribution of geographic variation projections onto canonical variable 1. The eigenvalue for canonical variable 1 is 1.00, while that for variable 2 is 0.19. The two together summarize 82.4% of the variance in the five characters. In the scatter diagram (Fig. 7), blocks with only single specimens are projected onto the canonical variables generated by using the other 29 blocks. As indicated in Table 5, the most important character in the canonical-variates analysis was postorbital width. (Fig. 8A). It has relatively small values in the northeastern portion of the range, and considerably larger values in other areas to the south, southwest, and west. The largest postorbital width measurements are found in specimens taken near the Hawaiian Islands (0802). The geographic configuration of this character is very similar to the general pattern exhibited by the first canonical variable (Fig. 8B). Canonical variable 1 and principal component I (Fig. 4) have similar geographic patterns. Canonical variable 2 does not reflect any particular geographic pattern. It basically contrasts three blocks (0711, 0802, and 0311) with the others, as indicated by these three being separated in the upper portion of Figure 7 from other blocks.

Mantel test for geographic patterning

Results of Mantel tests and matrix correlations comparing interblock character differences with geographic distances (in nautical miles) and with the reciprocals of geographic distances are presented in Table 6. Regional patterning, as indicated by a significant association with geographic distance, was found for 18 (60.0%) of the 30 characters. In these characters, the localities the farthest apart tended to exhibit the greatest morphological difference. Local patterning, which is judged based on a significant negative association between geographic distance-reciprocals and morphological differences, was found in 22 (73.3%) of the characters. Not unexpectedly, virtually all characters (i.e. all but one) exhib-

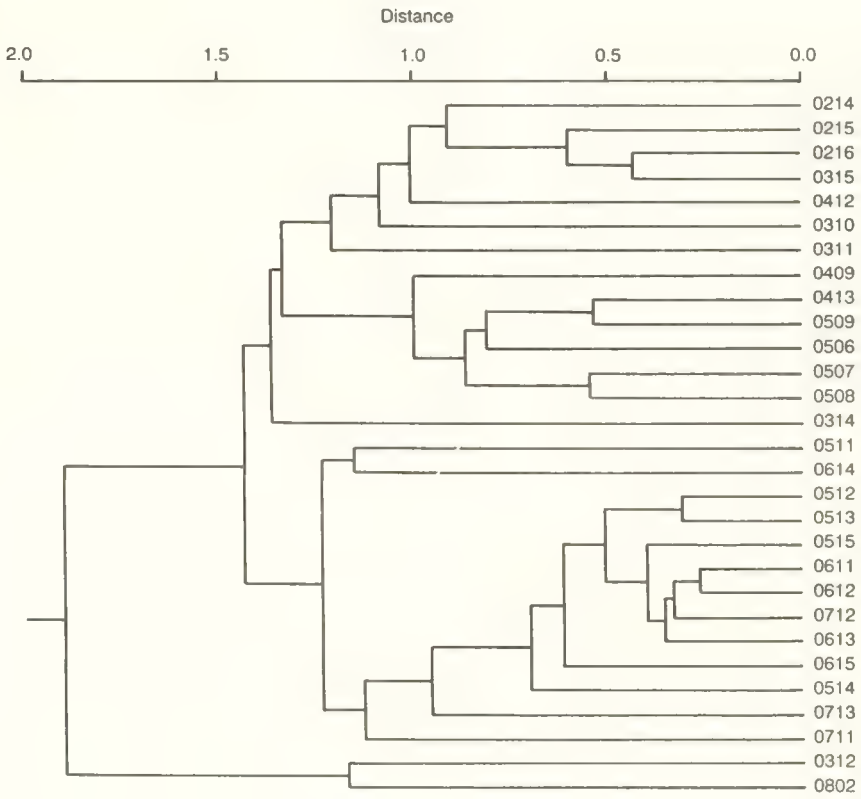

Figure 5

Distance phenogram summarizing UPGMA clustering of 29 latitude-longitude blocks based on 30 characters. Cophenetic correlation is 0.76.

Table 5

Canonical variates analysis of all specimens of *Stenella attenuata* from 29 latitude-longitude blocks.

Character[1]	*F*–value to enter	Order of entry	Coefficients[2] 1		2	
3 L. Rostrum (from Pterygoid)	2.88	4	0.0062	(0.0665)	−0.0731	(−0.7900)
9 Preorbital W.	9.19	1	0.1932	(0.8774)	0.0031	(0.3650)
14 L. Braincase	2.53	5	−0.0266	(−0.0851)	0.2243	(0.7179)
17 L. Temporal Fossa	2.84	3	−0.1113	(−0.4674)	0.0895	(0.3759)
18 W. Temporal Fossa	7.22	2	−0.1167	(−0.4305)	−0.0812	(−0.2996)
Constant			−13.5670		−18.3837	

[1] Abbreviations identified in Footnote 1 of Table 1.
[2] Unstandardized coefficients (with standardized values in parentheses) for canonical variates

iting a significant regional pattern also showed local patterning.

Our tests showed strong regional and local patterning for principal component I and canonical variable 1, whereas principal component II has significant local patterning (Table 6). Mantel tests and correlations confirm a point made earlier—that canonical variable 2 does not exhibit a systematic geographic pattern.

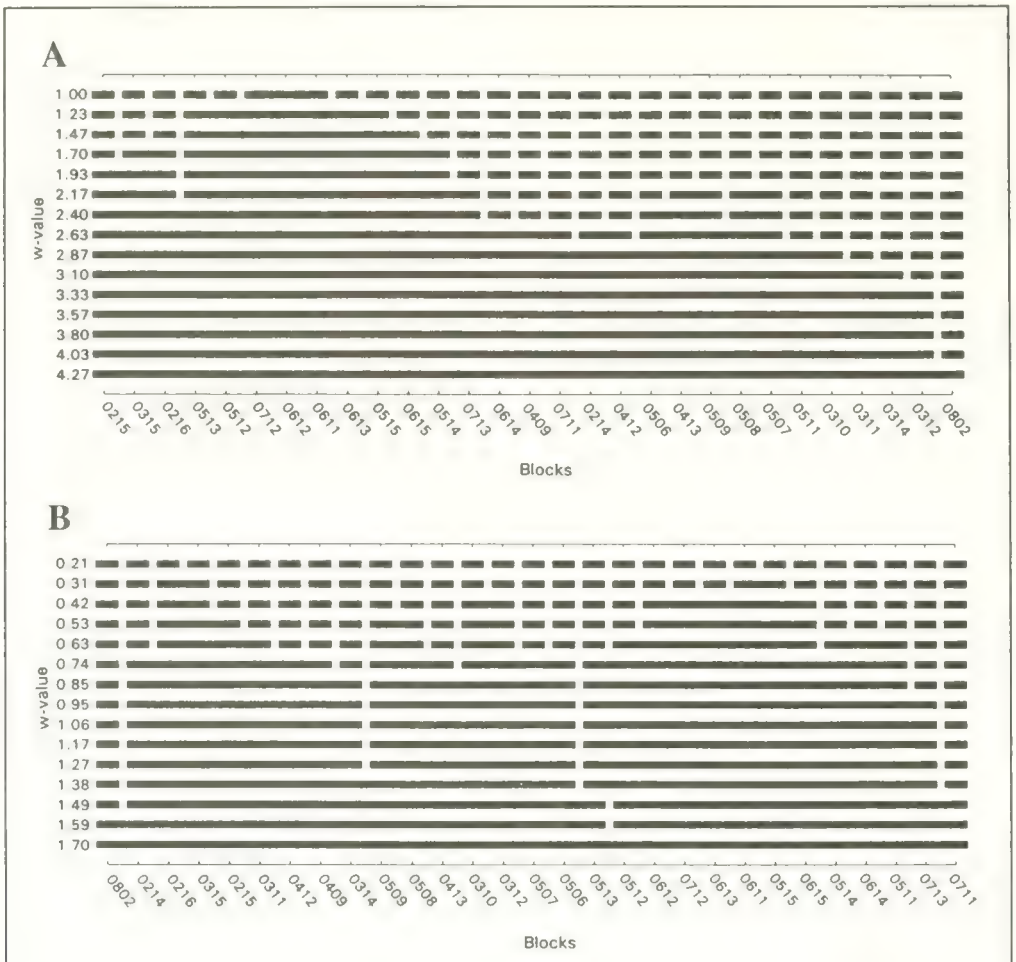

Figure 6

Modified skyline diagrams for 29 latitude-longitude blocks, indicating groups formed using function-point clustering procedures and based on: (**A**) all 30 characters; (**B**) five characters that, in combination, best discriminate among blocks (preorbital width, width of temporal fossa, length of temporal fossa, length of rostrum [from pterygoid], length of braincase). For given *w*-value (i.e. row), blocks connected in common line are in same cluster.

Morphological-environmental covariation

Douglas et al. (1992: fig. 9) included a dendrogram summarizing absolute correlations among 13 environmental variables (listed in Table 2) for blocks having either *S. attenuata* or *S. longirostris* or both. These variables were partitioned into five clusters. Sea current (N., winter) is separated by itself, whereas sea current (W., winter) and oxygen minimum layer (depth) form a second cluster, which groups with an assemblage of five variables involving surface measures of temperature, oxygen, and salinity (variables 6, 7, 8, 10, and 13). The fourth cluster has the two solar insolation variables (4 and 5), while the fifth includes three measures indicating water and thermocline depths (variables 3, 11, and 12).

A principal-components analysis was conducted to obtain variables that would summarize general environmental trends; three components were presented from Douglas et al. (1992: table 6). Highest loadings for environmental variables on principal component I included those for sea surface temperatures (variables 6, 7, and 8), particularly July temperatures. The correlation with sea surface temperature (annual variable) is negative. The second component reflected thermocline depth (variable 11 and 12), as well as water depth and surface salinity. The

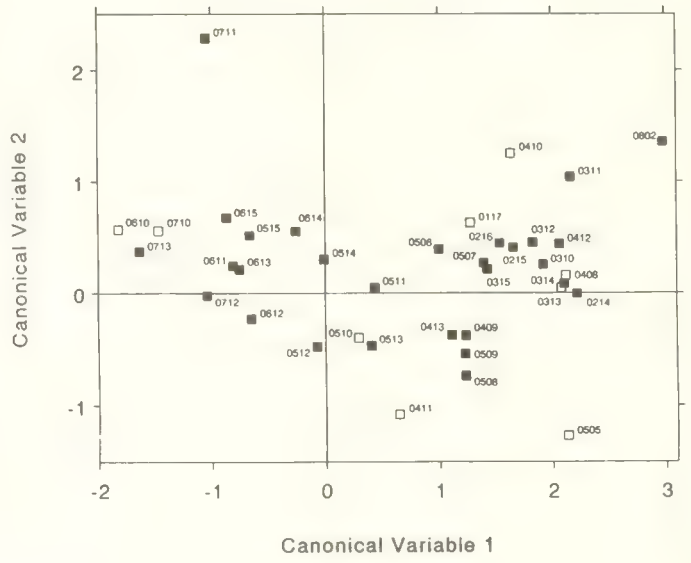

Figure 7

Projections of latitude-longitude blocks onto first two canonical variables based on 30 characters. Solid symbols indicate 25 blocks on which analysis was conducted. Open symbols represent blocks with only single specimens, which were projected onto axes generated from 29 blocks with two or more specimens.

third had relatively high loadings with the two characters involving solar insolation (variables 4 and 5). A more detailed description of character associations with the principal components is available in Douglas et al. (1992).

Projection values for environmental principal component I are summarized in Figure 9A for the 29 blocks with larger samples of *S. attenuata*. It reflects the fact that sea surface temperatures are considerably higher in northern than southern blocks, and that the northern blocks exhibit relatively little annual variation in surface temperatures. Block projections on environmental principal component II are portrayed in Figure 9B, which summarizes the increases in thermocline depth, water depth, and surface salinity as one proceeds west and south.

Correlations of morphologic variables, principal components, and canonical variables with environmental variables and environmental principal components are summarized in Table 7. The sea current measures (variables 1 and 2) have virtually no statistical association with morphological characters, while water depth (variable 3) has positive correlations with lengths and widths of the rostrum, as well as principal component I and canonical variable 1 (Table 7).

Solar insolation (Jan.), the fourth variable, has larger values in the south; values become smaller to the north. It has significant positive correlations with nine morphologic variables, and negative associations with six others. The negative associations with the two temporal fossa measures are particularly strong (width of temporal fossa summarized in Fig. 10A). This environmental variable has relatively high correlations with canonical variable 1 and principal component II (Table 7).

Not unexpectedly, the fifth variable, solar insolation (annual) exhibits high values at the equator. Readings are lower for blocks closer to either pole. It has few significant statistical associations with morphologic characters, although the negative correlations with length of braincase and width of temporal fossa (Fig. 10A) are relatively high (Table 7).

The sixth and seventh environmental measures (surface temperatures in January and July) have negative associations with a number of width measurements, as well as with a few length variables (Table 7). They have very strong positive correlations with temporal fossa measures. Figure 10 summarizes the values for sea surface temperature (July), as well as for the closely associated width of temporal fossa (r=0.799; the highest correlation of an environmental and a morphological variable). Sea surface temperature (annual variable), the eighth environmental variable, has significant correlations with relatively few morphologic characters (Table 7), although its pattern has affinities with those summarized by principal component II and canonical variable 1. Environmental variable 9, oxygen minimum layer (depth), shows very few statistically significant correlations with morphological measurements (Table 7).

Surface salinity, variable 10, exhibits strong covariation with numerous measurements, particularly those involving the anterior portion of the skull (Table 7). It also has high correlations with principal component I (Fig. 4) and canonical variable 1 (Fig. 8B). Salinity, which was depicted in Douglas et al. (1992: fig. 13B) for *S. longirostris* blocks, shows east-west changes from lower to higher values at a given latitude, as well as a north-to-south trend of increasing values (below 15°N).

The eleventh variable, thermocline depth (winter), is summarized in Figure 11B. It has positive correlations with 12 morphological measures and a negative correlation with 1 character. The correlation of this environmental variable with skull width (at parietals), shown in Figure 11A, is 0.610. Variable

12, thermocline depth (summer), has strong positive correlations with a large number of variables, particularly those reflecting measurements in the anterior portion of the skull. Given its covariation with water depth, it is not surprising that thermocline depth (winter) has significant correlations with principal component I and canonical variable 1. Surface dissolved oxygen (variable 13) has only a few weak statistical associations with morphological characters.

Environmental principal component I (Fig. 9A) has a pattern similar to those for sea surface temperatures in January and July (variables 6 and 7). The highest correlation (0.733) of this component is with width of temporal fossa (Fig. 10A). The second environmental component (Fig. 9B) is strongly associated with numerous characters (Table 7), reflecting the general trends from the northeast to the west, southwest, and south. The third component, which is negatively associated with canonical variable 2 (Table 7), has only one strong association with a morphological variable, that being with tooth width (r=–0.680; Table 7). The third environmental component exhibits decreasing values as one moves away from the equator. Tooth width shows an opposite pattern, which is particularly emphasized with the relatively thick teeth in specimens from the Hawaiian Islands (block 0802).

In Table 8, Mantel t-values and matrix correlations are provided for associations of environmental variables (including environmental principal components) with the five morphologic characters selected for inclusion during the canonical-variates analysis. With this approach, covariation patterns are assessed on the basis of difference values between all block pairs. Preorbital width shows a strong association with water depth, the two measures of solar insolation, the sea surface temperatures in January and July, oxygen minimum layer (depth), and surface salinity (Table 8). It also exhibits a pattern that is statistically associated with all three environmental components. The two measures of the temporal fossa show concordance with patterns for solar insolation (January, as well as annual), all sea surface temperature measures, oxygen minimum layer (depth), surface salinity, and the first environmental principal component. The length of temporal fossa also has a weak statistical

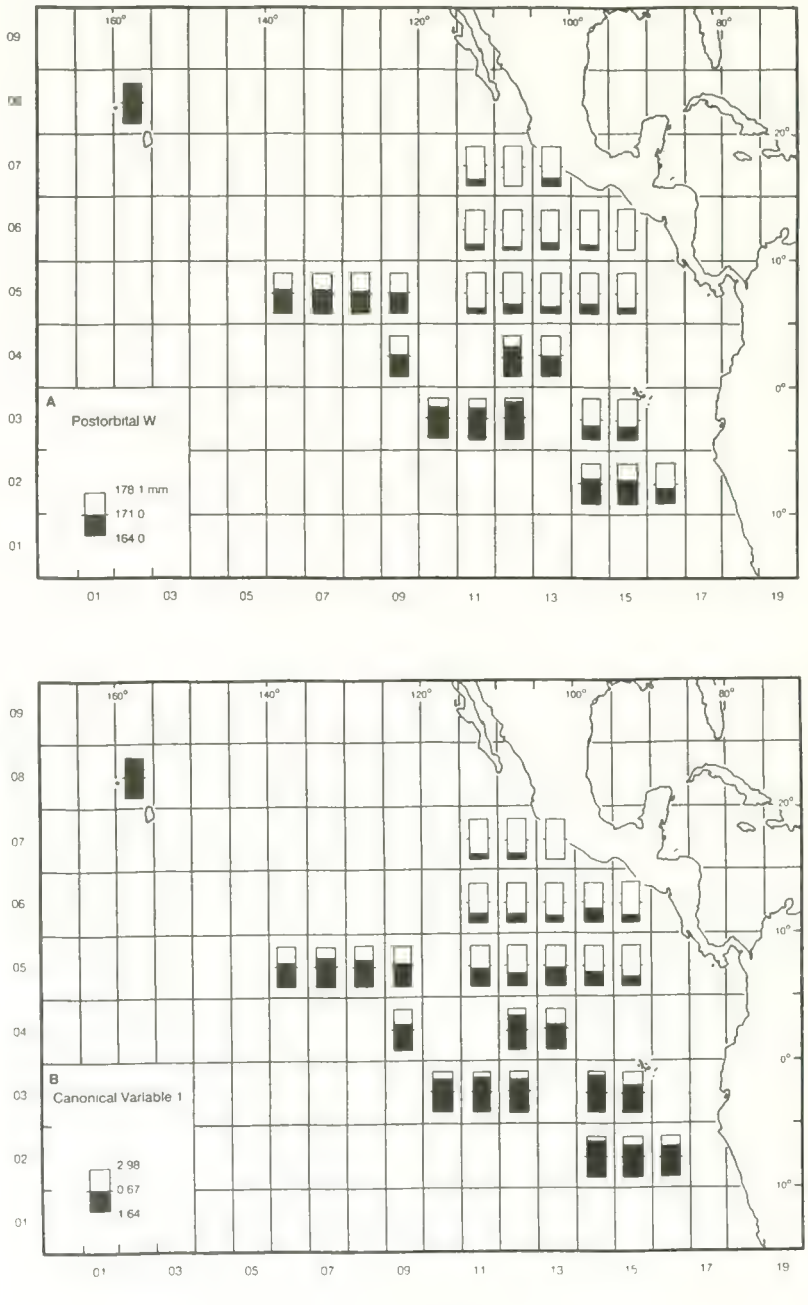

Figure 8

Geographic variation in (**A**) postorbital width and (**B**) canonical variable 1. Darkened part of bar indicates value for particular latitude-longitude block.

association with environmental component III. Table 8 indicates that the pattern for length of rostrum (from pterygoid) is associated statistically with those for water depth and thermocline depth (summer). This morphologic character also is shown to have geographic patterning statistically similar to that exhibited by environmental components II and III. For length of braincase, the Mantel tests were significant (but weak) only for sea current (N., winter) and solar insolation (Jan.). The strongest association of length of braincase is with environmental component III; its pattern also is linked statistically to the second environmental component.

Table 6

Association of interlocality character differences with geographic distances (in nautical miles) and the reciprocals of these distances. Results from Mantel tests (t) and matrix correlations (r) for offshore *Stenella attenuata*.

	Distance		Reciprocal of distance	
Character[1]	t	r	t	r
1 Condylobasal L.	4.19***	0.460	−4.19***	−0.303
2 L. Rostrum (from Base)	4.34***	0.449	−4.45***	−0.310
3 L. Rostrum (from Pterygoid)	3.59***	0.352	−4.10***	−0.276
4 W. Rostrum (at Base)	4.53***	0.493	−5.07***	−0.365
5 W. Rostrum (at 1/4 L.)	4.11***	0.446	−4.84***	−0.348
6 W. Rostrum (at 1/2 L.)	3.76***	0.413	−4.73***	−0.343
7 W. Premax. (at 1/2 L.)	1.28	0.134	−2.88**	−0.203
8 W. Rostrum (at 3/4 L.)	3.14**	0.347	−4.11***	−0.300
9 Preorbital W.	5.00***	0.464	−6.83***	−0.445
10 Postorbital W.	4.61***	0.397	−6.66***	−0.416
11 Skull W. (at Zygomatic P.)	4.22***	0.380	−6.21***	−0.398
12 Skull W. (at Parietals)	4.81***	0.583	−4.34*	−0.336
13 Ht. Braincase	1.81	0.227	−1.81	−0.143
14 L. Braincase	2.60**	0.339	−1.85	−0.151
15 Max. W. Premax.	1.64	0.159	−3.53***	−0.236
16 W. External Nares	0.78	0.066	−1.38	−0.085
17 L. Temporal Fossa	1.49	0.152	−3.13**	−0.216
18 W. Temporal Fossa	0.90	0.097	−2.86**	−0.206
19 Orbital L.	−0.25	−0.031	−0.35	−0.027
20 L. Antorbital P.	0.89	0.078	−3.65***	−0.229
21 W. Internal Nares	0.44	0.046	−1.09	−0.077
22 L. Up. Toothrow	4.08***	0.422	−3.93***	−0.274
23 No. Teeth (Up. Lf.)	1.57	0.173	−1.68	−0.123
24 No. Teeth (Up. Rt.)	3.03**	0.296	−3.68***	−0.247
25 No. Teeth (Low. Lf.)	1.75	0.188	−1.89	−0.135
26 No. Teeth (Low. Rt.)	2.44*	0.283	−2.39*	−0.180
27 L. Low. Toothrow	2.99**	0.364	−3.20**	−0.249
28 Ht. Ramus	1.74	0.181	−1.69	−0.116
29 Tooth W.	3.36***	0.398	−3.82***	−0.292
30 L. Ramus	3.02**	0.361	−2.88**	−0.221
Component I	4.54***	0.474	−5.51***	−0.386
Component II	1.42	0.122	−2.75**	−0.172
Canonical Variable 1	3.76***	0.289	−6.69***	−0.393
Canonical Variable 2	1.11	0.143	−1.47	−0.119

* $P<0.05$; **$P<0.01$, ***$P < 0.001$.
[1] Abbreviations identified in Footnote 1 of Table 1.

Interspecific comparisons

The study by Douglas et al. (1992) reported comparable statistical analyses on skulls of *S. longirostris*, a dolphin species that overlaps broadly with *S. attenuata* in the eastern tropical Pacific. The projections onto the first two principal components for *S. attenuata* were evaluated against projections on the two components obtained for *S. longirostis* (for summary information on these components, see Fig. 3 and Table 4 for offshore *S. attenuata*, and fig. 3 and table 3 of Douglas et al. [1992] for *S. longirostris*). A strong correspondence exists between the first principal components for the two species, as indicated by product-moment correlations, Mantel t-tests, and matrix correlations comparing the component projections. The second principal components for the two studies are not similar (Table 9); they summarize different general trends in variation.

A similar interspecific comparison was made of projections of the 16 blocks onto canonical variables (Table 9). The first canonical variable for *S. attenuata* and that for *S. longirostris* are virtually identical, reflecting highly concordant geographic patterns for the two species (Table 9). While block projections on the first canonical variables for the two species were very similar, the actual characters incorporated into the canonical variables are not the same (see our Table 5 and table 4 of Douglas et al. 1992). Of the five characters entered for each species, only length of rostrum (from pterygoid) was present in both character sets. However, the first and most important character entered into the analyses—preorbital width for *S. attenuata* and postorbital width for *S. longirostris* are highly correlated (see close association of these two characters in *S. attenuata* indicated in Fig. 2); because these two characters exhibit very similar variation pat-

terns, a canonical-variates analysis typically would not select both for inclusion, since they provide basically the same information for separating blocks.

The second canonical variables for the two studies also were compared (Table 9). They showed no statistical association.

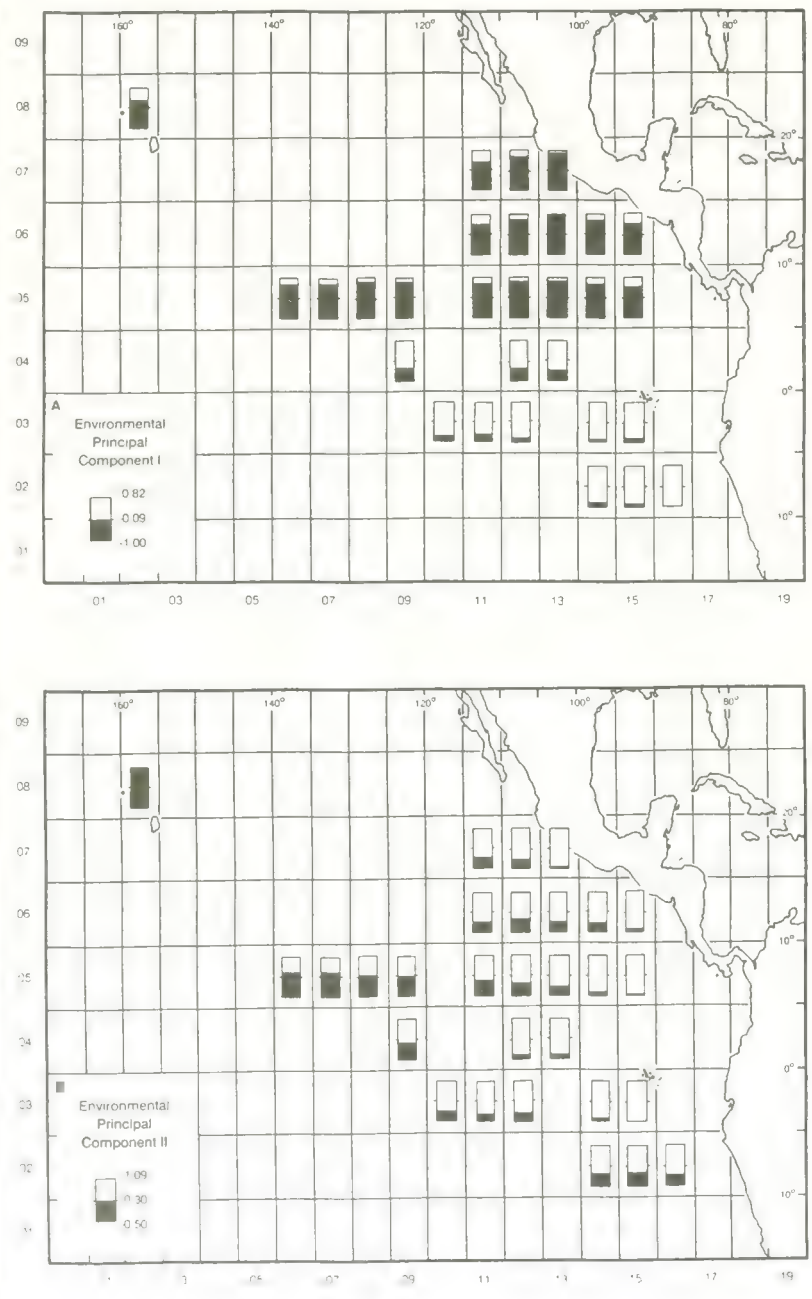

Figure 9

Geographic variation in environmental variables as summarized in (**A**) principal component I and (**B**) principal component II. Darkened part of bar indicates value for particular latitude-longitude block.

Table 10 includes results of Mantel tests, matrix correlations, and product-moment correlations of interspecific comparisons for individual morphological characters. Thirteen of the 30 *t*-values for Mantel tests of interlocality differences for the same character in the two species were significant, while 15 of 30 product-moment correlations indicated statistical associations. Nine of 11 characters with positive correlations were width measures. Furthermore, a tenth (length of antorbital process) is essentially a width character as well (for illustration of measurement, see Schnell et al. 1985). The two characters involving upper tooth counts, as well as length of temporal fossa, exhibited significant negative correlations. For *S. attenuata*, upper tooth counts tend to be higher for the western blocks (but not for the Hawaiian Island block), whereas in *S. longirostris*, higher upper tooth counts are found in the Hawaiian and eastern blocks. The length of temporal fossa is greater in northern localities of *S. attenuata* (Fig. 10A), whereas the shorter fossae are found in northeastern blocks for *S. longirostris* (see Douglas et al. 1992: fig. 11).

Discussion

Sexual dimorphism

Schnell et al. (1985) conducted the most recent analysis of sexual dimorphism of *S. attenuata* in cranial morphology. They found statistically significant dimorphism for 23 of 36 characters. Our analyses used many of the same specimens, with some added and some deleted, and 30 of the same characters. For the 30 characters we analyzed, Schnell et al. (1985) found the same 22 to have statistical differences between sexes (one statistically significant character analyzed earlier was not used in our analysis). Results from the two studies on sexual dimorphism are essentially the same. Thus, for *S. attenuata*, our current findings simply update information in Schnell et

Table 7

Product-moment correlations of block means for morphological variables and components versus environmental variables and components based on 29 latitude-longitude blocks of offshore *Stenella attenuata*.[1]

	Environmental variable[3]													Environmental component		
Character[2]	1	2	3	4	5	6	7	8	9	10	11	12	13	I	II	III
1 Condylobasal L.			++							+	++	+++			+++	
2 L. Rostrum (from Base)			++								++	+++			+++	
3 L. Rostrum (from Pterygoid)			++							+	+	+++			++	
4 W. Rostrum (at Base)			++			--	-			+++	++	+++			+++	
5 W. Rostrum (at 1/4 L.)			++			---	--			+++	+	++		--	++	
6 W. Rostrum (at 1/2 L.)			+	+		---	---	+		+++		+		--	+	
7 W. Premax. (at 1/2 L.)			+	+		--	--			++		+		- -		
8 W. Rostrum (at 3/4 L.)			++	+		--	--			+++		+		-	+	
9 Preorbital W.			+++	+		---	---			+++	+	++		--	++	
10 Postorbital W.			+++	+		---	---			+++		++		--	++	
11 Skull W. (at Zygomatic P.)			++			---	---	+	-	+++		++		---	+	
12 Skull W. (at Parietals)				-	-						+++				++	
13 Ht. Braincase											++					
14 L. Braincase				--	---						++					- -
15 Max. W. Premax.				+		--	--			++		++		-		
16 W. External Nares	-															
17 L. Temporal Fossa				- - -	-	+++	+++	-		-		-	---	+++		
18 W. Temporal Fossa						+++	+++	---		---				+++		-
19 Orbital L.										++						
20 L. Antorbital P.				++		---	---	+	--	+++		+		---		
21 W. Internal Nares						--	--	+	-	++				-		
22 L. Up. Toothrow		-	+					-			++	+++			+++	
23 No. Teeth (Up. Lf.)	++												-			
24 No. Teeth (Up. Rt.)													-			+
25 No. Teeth (Low. Lf.)						++								+		
26 No. Teeth (Low. Rt.)						+										
27 L. Low. Toothrow			+								+	++			++	
28 Ht. Ramus																
29 Tooth W.																-
30 L. Ramus			+								++	+++			++	
Component I			++			---	--			+++	+	+++		-	++	
Component II				++		--	--	+++		+			++			
Canonical Variable 1			+++	+++	+	---	---	++		+++		++		---	+	
Canonical Variable 2																- -

[1] Blanks indicate nonsignificant correlations. Individual symbols refer to significant positive or negative correlations ($P<0.05$; greater than 0.367), double symbols indicate highly significant correlations ($P<0.01$; greater than 0.470), and triple symbols represent very highly significant correlations ($P<0.001$; greater than 0.580).

[2] Abbreviations identified in Footnote 1 of Table 1.

[3] Environmental variables: (1) Sea Current (N., winter); (2) Sea Current (W., winter); (3) water depth, (4) solar insolation (Jan.); (5) solar insolation (annual); (6) sea surface temp. (Jan.); (7) sea surface temp. (July); (8) sea surface temp. (ann. var.); (9) oxygen min. layer (depth); (10) surface salinity; (11) thermocline depth (winter); (12) thermocline depth (summer); and (13) surface dissolved oxygen.

al. (1985) to reflect a modified sample size and a reduced character set.

Douglas et al. (1992) analyzed sexual dimorphism in skull measures for *S. longirostris* from the eastern tropical Pacific. They found 15 of the 30 characters to be statistically different between sexes. Since *S. longirostris* samples are somewhat smaller, one might expect fewer significant differences in this species simply due to sample size. Nevertheless, inspection of the results indicates support for the conclusion reached by Douglas et al. (1986: 542–543) "that the degree of sexual dimorphism in spotted dolphins is greater than in spinner dolphins." They also pointed out that "the trends are basically the same for both species, suggesting that common behavioral and/or ecological factors are influencing sexual dimorphism in these dolphins."

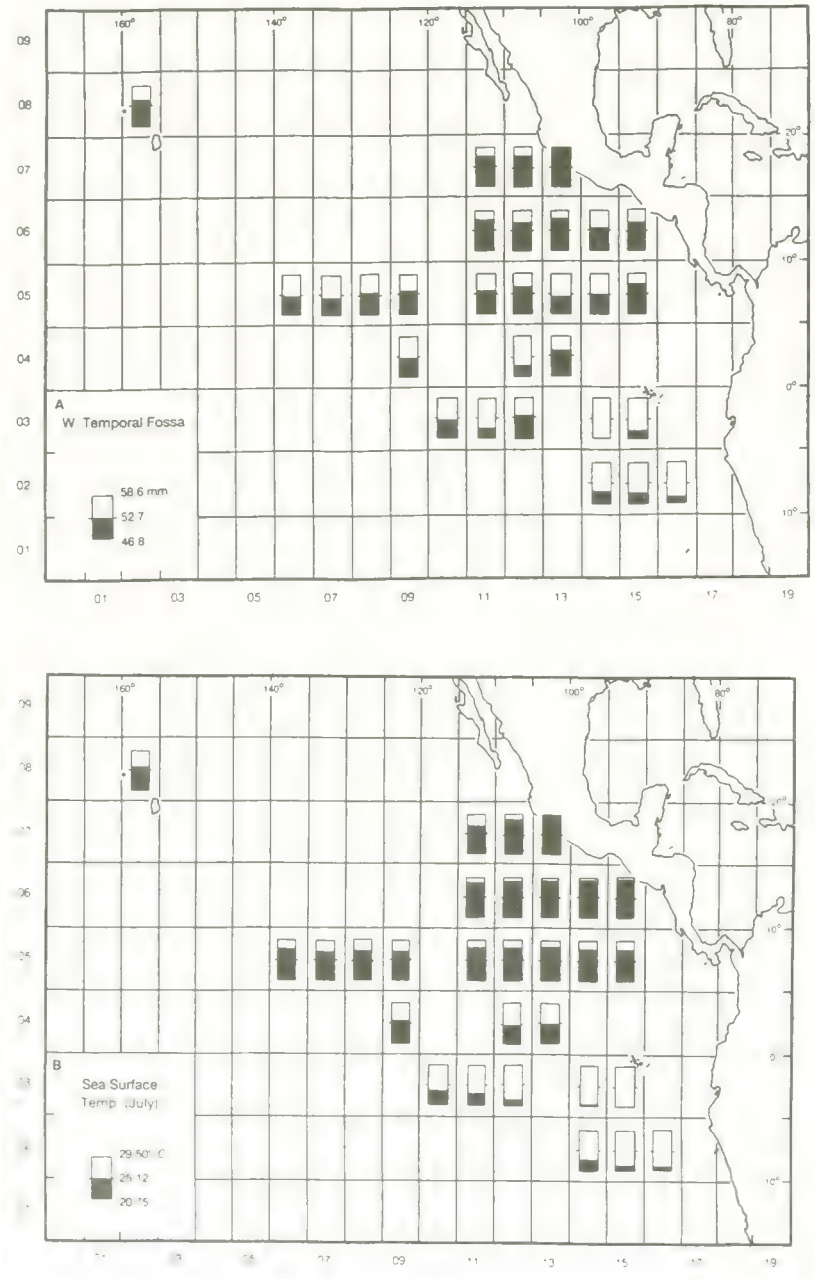

Figure 10

Geographic variation in (**A**) width of temporal fossa and (**B**) sea surface temperature (July). Darkened part of bar indicates value for particular latitude-longitude block.

Geographic variation

From an initial group of specimens, Perrin et al. (1979a) described differences between dolphin skulls available from southern areas and those from more northerly locations. Schnell et al. (1986), based on larger sample sizes, indicated that available information "strongly implies a significant degree of isolation between northern and southern forms." They did not have specimens from west of 125°W and called for additional material from west of 120°W to help clarify the relationship between southern *S. attenuata* and other populations, particularly in light of the notation by Perrin et al. (1979a) of similarities of specimens from the southern group with those from Hawaii. In the eastern portion of the range, the subdivision between northern and southern offshore *S. attenuata* found previously by Perrin et al. (1979a) and Schnell et al. (1986) was confirmed by our analyses with a geographically expanded specimen base. In general, blocks to the west (including those from the waters adjacent to Hawaii) are more like the southern blocks than blocks of the northeast. We found a general concentric pattern of geographic variation (see Fig. 8B), much like that established by Douglas et al. (1992) for the broadly overlapping *S. longirostris*. This also was suggested by Perrin et al. (1985).

Reilly (1990) provided some insight as to possible reasons why samples of *S. attenuata* and *S. longirostris* from the south, southwest,

and west would show close morphologic affinities. He analyzed large-scale dolphin distribution patterns and environmental patterns based on research-vessel surveys conducted in the eastern tropical Pacific from June through November, comparing his results with those of Au and Perryman (1985). Reilly's (1990) distributional comparisons between seasons indicated that along 10°N *S. attenuata* and *S. longirostris* occur in relatively high density west of 120°N during the summer. Furthermore, they were not in high densities along 4°N between 90 and 120°W, and along 6°N between 88 and 110°W—regions with relatively high concentrations of these two species in the winter (Au and Perryman, 1985). Reilly (1990) indicated that "One hypothesis suggested by these complementary changes is an intraregional, seasonal movement." Data from mark-recapture efforts (Perrin et al., 1979b; Hedgepeth[4]) are consistent with respect to the hypothesized direction of such migrations, although the distances are greater than those suggested by the very limited data from these studies. Reilly (1990) also noted that the suggested movement patterns are at least partially explainable based on seasonal atmospheric and oceanographic changes in the region.

Morphological-environmental covariation

In the earlier study of *S. attenuata*, Schnell et al. (1986) assessed environmental-morphological covariation for a similar, although not identical, set of environmental parameters. Since their investigation was restricted largely to eastern blocks, different findings with respect to covariation are possible. Schnell et al. (1986) noted that the strongest morphological-environmental associations involved solar insolation (Jan.). Sea surface temperatures also covaried with a number of morphological characteristics, as did oxygen minimum layer (depth).

The environmental principal components indicated that a number of environmental measures have a north-south component (see Fig. 9A), while others (particularly thermocline depth and water

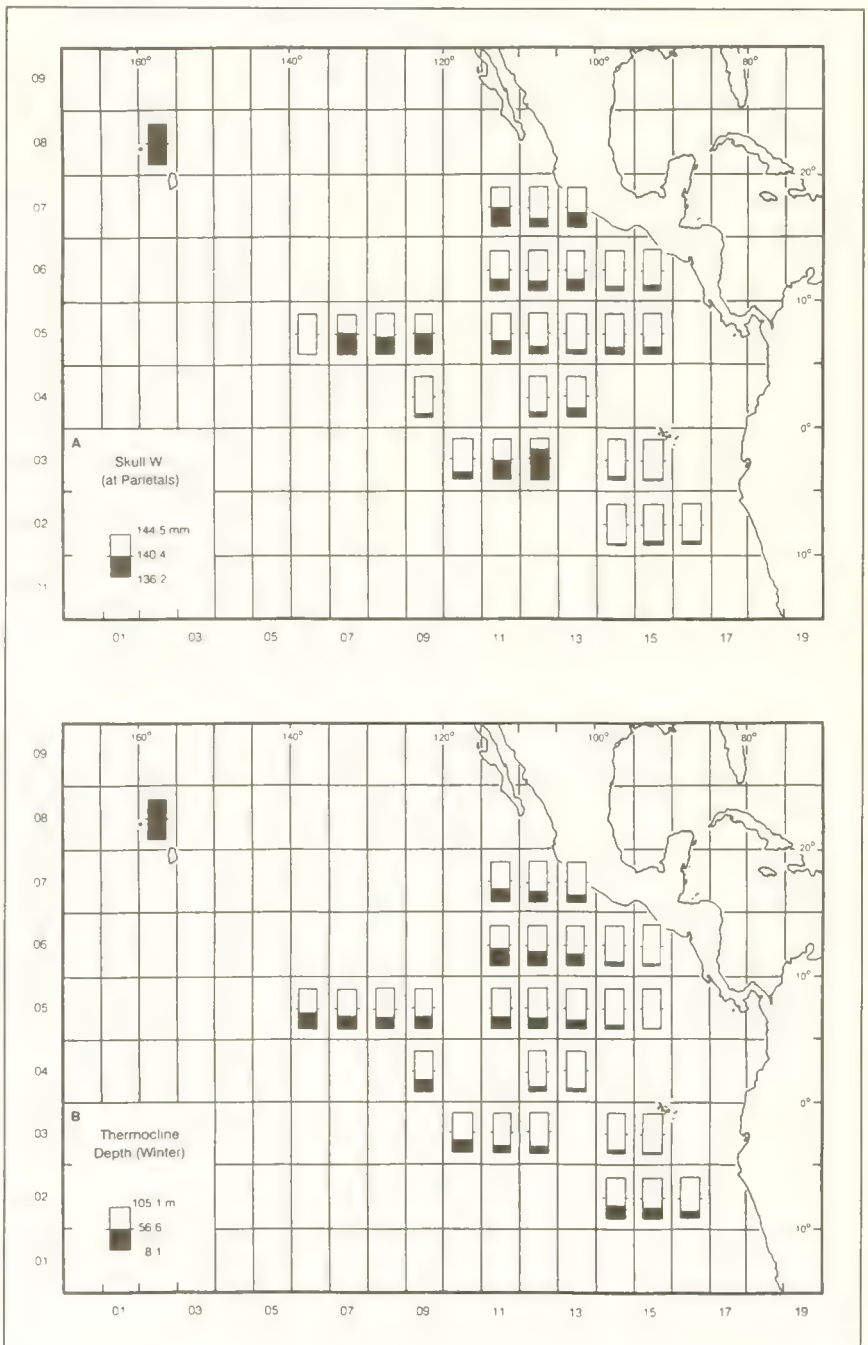

Figure 11

Geographic variation in (**A**) skull width (at parietals) and (**B**) thermocline depth (winter). Darkened part of bar indicates value for particular latitude-longitude block.

[4] Hedgepeth, J. B. 1985. Database for dolphin tagging operations in the eastern tropical Pacific, 1969–1978, with discussion of 1978 tagging results. Southwest Fisheries Center Admin. Rep. No. LJ-85-03, 40 p.

Table 8

Results of Mantel tests (t) and matrix correlations (r) for offshore *Stenella attenuata*. Comparison of interlocality differences for 13 environmental variables and 3 environmental components against those for five morphological variables selected in canonical-variates analysis.

Environmental variable	Preorbital width		Width of temporal fossa		Length of temporal fossa		Length of rostrum (from pterygoid)		Length of braincase	
	t	r	t	r	t	r	t	r	t	r
1 Sea Current (N.,winter)	−1.34	−0.114	2.43*	0.318	−0.20	−0.026	0.67	0.085	2.41*	0.322
2 Sea Current (W.,winter)	0.02	0.001	−1.95	−0.139	−1.68	−0.119	1.94	0.136	0.82	0.059
3 Water Depth	4.12***	0.259	−0.45	−0.033	−1.08	−0.080	3.24**	0.236	1.17	0.088
4 Solar Insolation (Jan.)	7.38***	0.466	6.39***	0.479	6.47***	0.481	−0.56	−0.041	−2.29*	−0.173
5 Solar Insolation (ann.)	7.58***	0.502	2.85**	0.238	2.91**	0.241	0.68	0.056	−0.84	−0.071
6 Sea Surface Temp. (Jan.)	5.53***	0.371	5.71***	0.493	4.70***	0.401	−1.15	−0.097	−1.43	−0.125
7 Sea Surface Temp. (July)	5.59***	0.369	6.97***	0.579	4.08***	0.335	−0.94	−0.076	−1.30	−0.109
8 Sea Surface Temp. (ann. var.)	1.69	0.114	6.23***	0.547	2.87**	0.249	−0.74	−0.064	−0.82	−0.073
9 Oxygen Minimum Layer (depth)	4.18***	0.236	3.60***	0.191	3.75***	0.200	−0.56	−0.030	−0.79	−0.042
10 Surface Salinity	9.52***	0.594	5.31***	0.386	4.66***	0.337	0.32	0.023	−1.20	−0.088
11 Thermocline Depth (winter)	0.40	0.026	0.90	0.070	1.88	0.144	0.20	0.016	−0.39	−0.031
12 Thermocline Depth (summer)	1.21	0.085	−0.07	−0.007	0.84	0.079	2.60**	0.240	0.00	0.000
13 Surface Dissolved Oxygen	−1.85	−0.147	0.76	0.089	1.83	0.211	−0.40	−0.045	−0.01	−0.001
Environmental Component I	3.71***	0.238	6.75***	0.476	4.57***	0.309	−1.69	−0.111	−1.31	−0.104
Environmental Component II	3.77***	0.364	−0.26	−0.030	0.39	0.041	3.45***	0.352	2.63**	0.359
Environmental Component III	4.64***	0.449	0.52	0.059	2.36*	0.252	2.22*	0.227	4.54***	0.623

*$P<0.05$; **$P<0.01$; ***$P<0.001$.

depth) show trends from the east to the west, southwest, and south. Not unexpectedly, a mosaic of variation patterns is present in the suite of morphologic characters we assessed. Some, like width of temporal fossa (Fig. 10A), align closely with environmental variables—such as sea surface temperature (July) (Fig. 10B)—subsumed under environmental component I (Fig. 9A). Others, like skull width (at parietals) (Fig. 11A), display patterns similar to those of thermocline depth (winter) (Fig. 11B) and other environmental measures summarized by environmental component II (Fig. 10B). However, the overall, general morphological trend is reflected best by projections onto the first canonical variable based on morphologic data (Fig. 4), which has a relatively strong negative correlation with environmental component I and a weaker positive one with environmental component II.

By adding the more westerly blocks to the analysis, environmental-morphological covariation patterns that emerged, in some cases, were different from those reported by Schnell et al. (1986). For example, the previous statistically significant correlations they found for several morphologic characters with sea current (N., winter) and sea surface temperature (annual variation) were not repeated

in our expanded study. Likewise, strong associations with measures of solar insolation were substantially reduced for all but a few characters (i.e. length of braincase, length of temporal fossa, and width of temporal fossa; Table 7). Some characters, such as sea current (W., winter) and oxygen minimum layer (depth), did not have variation patterns in either study that corresponded to those for morphologic variables. Water depth, however, has significant correlations with more characters now that western blocks have been added. At least three environmental measures—sea surface temperature (Jan.), sea surface temperature (July) (Fig. 10B), and surface salinity—had relatively strong covariation patterns that stayed relatively constant through the two studies.

Availability in the future of better information on environmental variation and, possibly, on other relevant parameters reflecting environmental heterogeneity will allow researchers to analyze dolphin-environmental covariation in a more meaningful way. For example, better environmental data and more comprehensive information on dolphin feeding ecology could provide a basis for testable predictions concerning why certain morphological characters covary with specific environmental variables. Our admittedly descriptive analyses demonstrate some striking cases of dolphin-environmental covariation and, thus, provide initial guidance in terms of possible causal relationships that may be examined with greater sophistication by future investigators.

Interspecific covariation

In this paper we have presented statistical data for trends in geographic covariation of *S. longirostris* and *S. attenuata* skulls from 16 blocks for which samples of both species were available (brief comments on covariation were included by Douglas et al. 1992). Geographic patterns in 13 of the 30 morphological characters showed statistical correspondence based on Mantel tests, whereas

Table 9

Comparisons of principal component and canonical variable projections for offshore *Stenella attenuata* and *S. longirostris* based on corresponding data for 16 latitude-longitude blocks.

	Principal component		Canonical variable	
Statistic	I	II	1	2
Product-moment correlation	0.745***	0.289	0.896***	–0.328
Mantel *t*-value	3.46**	0.32	6.65***	1.62
Matrix correlation	0.528	0.039	0.741	0.204

*$P<0.05$; **$P<0.01$; ***$P<0.001$. *P*-values for Mantel tests based on number of times permutational Z-values less than or equal to observed *Z*-values (one-tailed test).

Table 10

Results of Mantel tests, matrix correlations, and product-moment correlations for 16 overlapping latitude-longitude blocks of offshore *Stenella attenuata* and *S. longirostris*. Comparison of interlocality differences for 30 morphological variables.

Character[1]	Mantel *t*-value	Matrix correlation	Product-moment correlation
1 Condylobasal L.	1.21	0.184	0.256
2 L. Rostrum (from Base)	1.28	0.178	0.159
3 L. Rostrum (from Pterygoid)	0.55	0.074	0.150
4 W. Rostrum (at Base)	4.65***	0.626	0.837***
5 W. Rostrum (at 1/4 L.)	4.14***	0.337	0.693**
6 W. Rostrum (at 1/2 L.)	4.57***	0.495	0.775***
7 W. Premax. (at 1/2 L.)	–0.49	–0.066	0.351
8 W. Rostrum (at 3/4 L.)	1.01	0.120	0.540*
9 Preorbital W.	5.70***	0.737	0.865***
10 Postorbital W.	6.24***	0.693	0.861***
11 Skull W. (at Zygomatic P.)	6.37***	0.732	0.883***
12 Skull W. (at Parietals)	2.71**	0.446	0.616*
13 Ht. Braincase	0.60	0.093	0.294
14 L. Braincase	2.91*	0.494	0.613*
15 Max. W. Premax.	2.88**	0.318	0.675**
16 W. External Nares	–0.64	–0.073	0.224
17 L. Temporal Fossa	0.79	0.088	–0.499*
18 W. Temporal Fossa	0.62	0.077	–0.443
19 Orbital L.	0.92	0.148	0.383
20 L. Antorbital P.	4.10**	0.396	0.658**
21 W. Internal Nares	1.61	0.205	0.613*
22 L. Up. Toothrow	1.19	0.165	0.069
23 No. Teeth (Up. Lf.)	2.98**	0.501	–0.753***
24 No. Teeth (Up. Rt.)	2.99**	0.517	–0.691**
25 No. Teeth (Low. Lf.)	0.03	0.004	–0.223
26 No. Teeth (Low. Rt.)	0.66	0.104	–0.428
27 L. Low. Toothrow	0.59	0.090	0.015
28 Ht. Ramus	2.34*	0.298	0.408
29 Tooth W.	0.20	0.038	–0.260
30 L. Ramus	0.70	0.111	0.174

* $P<0.05$; **$P<0.01$; ***$P<0.001$. *P*-values for Mantel tests based on number of times permutational *Z*-values less than or equal to observed *Z*-values (one-tailed test).
[1] Abbreviations identified in Footnote 1 of Table 1.

product-moment correlations were significant for 15 characters. Some of these associations were very strong (i.e. correlations as high as 0.883; see Table 10). Given that we are comparing two species, entities that have independent gene pools, the most likely explanation for common positive trends in morphologic covariation is that the two species are being subjected to similar forces of natural selection.

However, we found several striking examples where covariation was negative. A significant negative association was found for length of temporal fossa, while the negative correlation for width of temporal fossa was nearly significant statistically. The number of upper teeth (characters 23 and 24) also show significant negative correlations (Table 10). Muscles associated with the feeding apparatus are positioned in the temporal fossa; obviously, tooth numbers could be related to prey types taken. One suspects that the presence of antithetical trends in these particular skull characteristics is a result of competitive interactions involving these two interacting species. This may be an example of ecological character displacement related to differences in feeding and food types taken (Perrin, 1984). Certainly, the two species are found in close association over much of the eastern tropical Pacific (Au and Perryman, 1985; Reilly, 1990); 49% of *S. attenuata* schools included some *S. longirostris*, while 73% of the schools of the less common *S. longirostris* included *S. attenuata* (Reilly, 1990).

The information available to date indicates that spinner and spotted dolphins may have different feeding habits or preferences in areas of co-occurrence in the eastern tropical Pacific. Based on analysis of stomach contents of spinner and spotted dolphins captured together in purse-seine hauls in the tuna fishery, Perrin et al. (1973) concluded tentatively that while some prey species are taken by both, spinner dolphins in the mixed-species associations specialize in small mesopelagic fishes (mainly myctophids and gonostomatids) and squids, whereas the spotted dolphins consume larger and more epipelagic species such as flying fishes, small scombroids (e.g. *Auxis* sp.), and larger squids. In addition, state of digestion of the stomach contents indicted that the spinner and spotted dolphins had fed at different times of the day. Stomachs of a spotted dolphin from Hawaii, where the two species do not school together, and from two spotted dolphins from the far western portion of the range in the eastern Pacific, where the mixed species associations are less common than in the core area of the tuna fishery off Mexico and Central America (Au and Perryman, 1985; fig. 11), contained a large proportion of small mesopelagic species like those eaten by the spinner dolphin in the mixed species associations farther to the east. This geographic variation in feeding habits may reflect resource partitioning where the two species associate closely, which in turn may be manifested in morphological character displacement.

Genetic subdivision, management units, and implications of cranial variation

The results suggest that gene flow is not uniform throughout the range of *S. attenuata* in the eastern Pacific; the morphological heterogeneity probably reflects genetic subdivision, a conclusion also reached as a result of the earlier study by Schnell et al. (1986). A similar inference was drawn by Douglas et al. (1992) based on morphologic studies of *S. longirostris*. For *S. attenuata*, we found that 93.3% of the 30 morphologic characters had statistically significant geographic variation, with 60.0% exhibited regional patterning and 73.3% local patterning. This geographic partitioning of morphologic variance was demonstrable even with pooling of specimens taken over a number of months and years, a process that would tend to shroud such relationships.

The boundaries of management units presently employed (Perrin et al., 1985) are not fully consistent with the general pattern of morphologic variation described here. It appears that animals west of about 120°W longitude have greater affinity with those in the Southern Offshore management unit than they do with *S. attenuata* from the eastern portion of the present Northern Offshore unit, the unit in which they are presently included. Further, the present boundary between the Northern and Southern Offshore units, at 1°S latitude, is probably too far south; a boundary at about 5°N would be more consistent with the general pattern of cranial variation.

The proposed Northern Offshore unit bounded by 5°N and 120°W would be nearly congruent with the "conservation zone" suggested for *S. longirostris* (Perrin et al., 1991). This is to be expected based on the correlated trends of covariation with environmental variables; the two species, as they exist in this region, apparently are parts of an endemic fauna uniquely adapted to the far eastern tropical Pacific and, as such, are "evolutionarily significant units" (Dizon et al., 1992).

The cranial results are only one line of evidence useful for delineation of management units; others, such as patterns in movements, external morphology or life-history parameters, also should be taken into consideration. For example, other data may indicate that *S. attenuata* west of 120°W differ sig-

nificantly in some regard from those south of 5°N and should be managed separately (yielding three management units instead of the present two). Certainly, the specimens from the Hawaiian Islands are generally larger than those from the south, southwest, and west with which they have their closest morphologic affinity.

Note added in proof Based in part on the results and recommendations in this paper, the management unit boundaries for the offshore spotted dolphin in the eastern Pacific have been changed. The boundary of a new "Northeastern stock" runs south along the 120°W meridian to 5°N and then east to the mainland. Offshore spotted dolphins outside this zone to the west and south are now part of a "Western/Southern stock." February, 1994.

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Literature cited

Allen, R. A.
1985. Dolphins and the purse-seine fishery for yellowfin tuna. *In* J. R. Beddington, R. J. H. Beverton and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 236–252. Allen and Unwin, London, 354 p.

Au, D. W. K., and W. L. Perryman.
1985. Dolphin habitats in the eastern tropical Pacific. Fish. Bull. 83:623–643.

Dailey, M. D., and W. F. Perrin.
1973. Helminth parasites of porpoises of the genus *Stenella* in the eastern tropical Pacific, with descriptions of two new species: *Mastigonema stenellae* gen. et sp. n. (Nematoda:Spiruroidea) and *Zalophotrema pacificum* sp. n. (Trematoda: Digenea). Fish. Bull. 71:455–471.

Dixon, W. D. (chief ed.).
1990. BMDP statistical software. Vol. 1. Univ. California Press, Berkeley, CA.

Dizon, A. E., C. Lockyer, W. F. Perrin, D. P. DeMaster and J. Sisson.
1992. Rethinking the stock concept: a phylogenetic approach. Conserv. Biol. 6:24–36.

Douglas, M. E., G. D. Schnell, D. J. Hough, and W. F. Perrin.
1992. Geographic variation in cranial morphology of spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific Ocean. Fish. Bull. 90:54–76.

Douglas, M. E., G. D. Schnell, and D. J. Hough.
1984. Differentiation between inshore and offshore spotted dolphins in the eastern tropical Pacific Ocean. J. Mammal. 65:375–387.
1986. Variation in spinner dolphins (*Stenella longirostris*) from the eastern tropical Pacific Ocean: sexual dimorphism in cranial morphology. J. Mammal. 67:537–544.

Hall, M. A., and S. D. Boyer.
1987. Incidental mortality of dolphins in the eastern tropical Pacific tuna fishery in 1985. Rep. Int. Whal. Commn. 37:361–362.
1988. Incidental mortality of dolphins in the eastern tropical Pacific tuna fishery in 1986. Rep. Int. Whal. Commn. 38:439–441.
1989. Estimates of incidental mortality of dolphins in the eastern Pacific fishery for tropical tunas in 1987. Rep. Int. Whal. Commn. 39:321–322.
1990. Incidental mortality of dolphins in the tuna purse-seine fishery in the eastern Pacific Ocean during 1988. Rep. Int. Whal. Commn. 40:461–462.
1991. Incidental mortality of dolphins in the tuna purse-seine fishery in the eastern Pacific Ocean during 1989. Rep. Int. Whal. Commn. 41:507–509.
1992. Estimates of incidental mortality of dolphins in the purse-seine fishery for tunas in the eastern Pacific Ocean in 1990. Rep. Int. Whal. Commn. 42:529–531.

Katz, J. O., and F. J. Rohlf.
1973. Function-point cluster analysis. Syst. Zool. 22:295–301.

Mantel, N.
1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27:209–220.

Perrin, W. F.
1984. Patterns of geographical variation in small cetaceans. Acta Zool. Fennica 172:137–140.

Perrin, W. F., R. R. Warner, C. H. Fiscus, and D. B. Holts.
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish. Bull. 71:1077–1092.

Perrin, W. F., P. A. Sloan, and J. R. Henderson.
1979a. Taxonomic status of the 'southwestern stocks' of spinner dolphin, *Stenella longirostris*, and spotted dolphin, *S. attenuata*. Rep. Int. Whal. Commn. 29:175–184.

Perrin, W. F., W. E. Evans, and D. B. Holts.
1979b. Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969–1976. U.S. Dep. Commerce, NOAA Tech. Rep. NMFS SSRF-737, 14 p.

Perrin, W. F., M. D. Scott, G. J. Walker, F. M. Ralston, and D. W. K. Au.
1983. Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the Eastern Tropical Pacific, with an annotated catalog of data sources. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS, 65 p.

Perrin, W. F., M. D. Scott, G. J. Walker, and V. L. Cass.
1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. U.S. Dep. Commerce, NOAA Tech. Rep. NMFS 28, 28 p.

Perrin, W. F., P. A. Akin, and J. V. Kashiwada.
1991. Geographic variation in external morphology of the spinner dolphin, *Stenella longirostris*, in the eastern Pacific and implications for conservation. Fish. Bull. 89:411–428.

Reilly, S. B.
1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Mar. Ecol. Prog. Ser. 66:1–11.

Rohlf, F. J., J. Kishpaugh, and D. Kirk.
1979. NT-SYS. Numerical taxonomy system of multivariate statistical programs. State Univ. New York, Stony Brook, New York.

Schnell, G. D., M. E. Douglas, and D. J. Hough.
1985. Sexual dimorphism in spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific Ocean. Mar. Mamm. Sci. 1:1–14.

1986. Geographic patterns of variation in offshore spotted dolphins (*Stenella attenuata*) of the eastern tropical Pacific Ocean. Mar. Mamm. Sci. 2:186–213.

Sneath, P. H. A., and R. R. Sokal.
1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco.

Wirth, M., G. F. Estabrook, and D. F. Rogers.
1966. A graph theory model for systematic biology with an example for the Oncidiinae (Orchidaceae). Syst. Zool. 15:59–69.

Modeling oyster populations. IV: Rates of mortality, population crashes, and management*

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Abstract.—A time-dependent energy-flow model was used to examine how mortality affects oyster populations over the latitudinal gradient from Galveston Bay, Texas, to Chesapeake Bay, Virginia. Simulations using different mortality rates showed that mortality is required for market-site oysters to be a component of the population's size-frequency distribution; otherwise a population of stunted individuals results. As mortality extends into the juvenile sizes, the population's size frequency shifts toward the larger sizes. In many cases adults increase despite a decrease in overall population abundance. Simulations, in which the timing of mortality varied, showed that oyster populations are more susceptible to population declines when mortality is restricted to the summer months. Much higher rates of winter mortality can be sustained. Comparison of simulations of Galveston Bay and Chesapeake Bay showed that oyster populations are more susceptible to intense population declines at higher latitudes. The association of population declines with disease agents causing summer mortality and the increased frequency of long-term declines at high latitudes result from the basic physiology of the oyster and its population dynamics cycle. Accordingly, management decisions on size limits, seasons and densities triggering early closure must differ across the latitudinal gradient and in populations experiencing different degrees of summer and winter mortality relative to their recruitment rate. More flexible size limits might be an important management tool. When fishing is the primary cause of mortality, populations should be managed more conservatively in the summer. The latitudinal gradient in resistance to mortality requires more conservative management at higher latitudes and different management philosophies from those used in the Gulf of Mexico.

One of the unfortunate characteristics of oyster *Crassostrea virginica* populations is their susceptibility to periods of heavy mortality, which can extend from a few months to a few years in duration. Oyster population abundances drop precipitously during these times and may remain low for extended periods (Schlesselman, 1955; Engle, 1956; Laird, 1961; Engle and Rosenfield, 1962). Why populations decline over several years or crash over shorter periods of time can usually be explained by killing floods (Andrews et al., 1959; Soniat and Brody, 1988; Soniat et al., 1989) or disease epizootics (Needler and Logie, 1947; Andrews and Hewatt, 1957; Mackin and Hopkins, 1962) although predators and overfishing have occasionally received some credit (Moore and Pope, 1910; Menzel et al., 1957; Quast et al., 1988).

A review of the literature shows that declines and crashes in oyster populations have some interesting characteristics (Mackin and Wray, 1950; Mackin et al., 1950; Menzel, 1950, a and b; Menzel and Hopkins, 1953; Owen, 1953; Gunter, 1955; Mackin and Sparks, 1962; Hofstetter et al., 1965; Copeland and Hoese, 1966; Hofstetter, 1966; Gilmore et al., 1975; and previously cited references):

1 With the exception of killing floods, the times of the year with the most intense mortality are usually restricted to the summer and early fall and to areas of higher salinity. Warm temperatures and high salinities promote the growth of the disease-producing organisms *Perkinsus marinus* and *Haplosporidium nelsoni* (Ray and Chandler, 1955; Andrews and Hewatt, 1957) and predation by such pests as the oyster drill, *Thais haemastoma* (Garton and Stickle, 1980; Stickle, 1985).
2 Population crashes or significant declines have been documented throughout the oyster's latitudinal range. However, except for permanent changes in salinity,

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owing to levee building for instance (Mackin and Hopkins, 1962), population recovery rates appear to be more rapid at lower latitudes (compare Owen, 1953; Hofstetter, 1983; Stanley and Sellers, 1986; Mackenzie, 1989).

3 Major population crashes resulting in long-term loss or decline of the *C. virginica* fishery have occurred almost exclusively along the northeast coast of North America. Moreover, significant population declines occurred earlier in the century at higher latitudes (viz. Canada, 1910s, Mid-Atlantic area, 1950s; Delaware and Chesapeake Bays, 1980s) (Stanley and Sellers, 1986; Mountford and Reynolds, 1988; Mackenzie, 1989; and others referenced previously), although more than one significant population has declined in some areas.

These trends in oyster population dynamics gleaned from the literature are not well documented. Much literature is anecdotal and significant exceptions do exist. Nevertheless, taken as a whole, these trends suggest two hypotheses: 1) a latitudinal gradient in susceptibility to population crashes exists in oyster populations; and 2) as temperature varies both latitudinally and seasonally, temperature, through its effect on oyster physiology (e.g. Koehn and Bayne, 1989), may determine the susceptibility of oyster populations to potentially destabilizing episodes of mortality.

In this study, we tested these hypotheses using a population dynamics model. The results of the modeling exercise were then used to examine some basic decisions required for fishery management; viz. the timing and length of the fishing seasons and the size limits set for the fishery to obtain a maximum sustainable yield (e.g. Glude, 1966; Hofstetter and Ray, 1988; Young and Martin, 1989).

The model

Perspective and basic characteristics

The oyster population model shown in Figure 1 is designed to investigate the dynamics of the post-settlement phase of the American eastern oyster's, *Crassostrea virginica*, life from newly settled juvenile through adulthood. The model consists of a system of ten coupled ordinary differential equations, with each equation representing a size class of oyster; however, the ten size classes are not evenly divided across the length or biomass spectrum (Table 1). Size class 1 includes newly settled juveniles (Dupuy et al., 1977). Size class 10 corresponds to oysters that are larger than those normally found in natural populations. The boundaries between size classes 4 and 5, 5 and 6, and 6 and 7 represent size limits that have been used or considered for market-size oysters: 2.5 in; 3.0 in and 3.5 in, respectively. We define adults, individuals capable of spawning, as individuals weighing more than 0.65 g ash-free dry weight, about 50 mm in length (Hayes and Menzel, 1981). Therefore, size classes 1 to 3 are juveniles.

Table 1

Biomass and length dimensions of the oyster *Crassostrea virginica* size classes used in the model. Biomass is converted to size using the relationship given in White et al. (1988).

Model Size class	Biomass (g ash-free dry wt)	Length (mm)
1	1.3×10^{-7} – 0.028	0.3 – 25.0
2	0.028 – 0.10	25.0 – 35.0
3	0.10 – 0.39	35.0 – 50.0
4	0.39 – 0.98	50.0 – 63.5
5	0.98 – 1.94	63.5 – 76.0
6	1.95 – 3.53	76.0 – 88.9
7	3.53 – 5.52	88.9 – 100.0
8	5.52 – 7.95	100.0 – 110.0
9	7.95 – 12.93	110.0 – 125.0
10	12.93 – 25.91	125.0 – 150.0

All calculations were done in terms of energy in $cal \cdot m^{-2}$. When necessary, oyster energy is converted to oyster biomass by using a caloric conversion of 6100 $cal \cdot g$ dry wt^{-1} for oysters (Cummins and Wuycheck, 1971) and biomass to an approximate length by using White et al.'s (1988) biomass-length conversion. To calculate any gain, loss, or transfer of energy (or biomass) between size classes, an additional conversion was made to express the gain, loss or transfer in terms of a specific rate (day^{-1}) which was then multiplied by the caloric quantity in a size class. Transfers between size classes were scaled by the ratio of the average weight of the current size class (in g dry wt or cal) to that of the size class from which energy was gained or to which energy was lost. This ensured that the total number of individuals in the model was conserved, in the absence of recruitment and mortality. Because, the size classes in the model are not equivalent in dimension, each specific rate for each transfer between size classes was scaled by the ratio between the two size classes:

$$\text{for transfers up:} \quad W_j/(W_{j+1}-W_j)$$
$$\text{for transfers down:} \quad W_j/(W_j-W_{j-1}),$$

where W is the median biomass (in g dry wt) in size class j. For simplicity, we will not include any of these conversions and scaling factors in the equations given subsequently.

Governing equation

The change in oyster standing stock with time in each size class (O_j) is the result of changes in net production (NP_j), taken to be the sum of the production of somatic (P_{gj}) and reproductive (P_{rj}) tissue, and the addition of individuals from the previous size class or loss to the next largest size class by growth. Following White et al. (1988), net productivity is assumed to be the difference between assimilation (A_j) and respiration (R_j),

$$NP_j = P_{gj} + P_{rj} = A_j - R_j. \quad (1)$$

Accordingly,

$$\frac{dO_j}{dt} = P_{gj} + P_{rj} + (\text{gain from } j-1) - (\text{loss to } j+1) \quad (2)$$

for j = 1,10 recognizing P_{rj} = 0 for j = 1,3.

Resorption of either gonadal or somatic tissue results in loss of biomass. When NP_j<0, oysters lose biomass and transfer into the next lower size class. This is an important difference between our size class model and a size class model based on linear dimensions; shell size does not change, however biomass does during periods of negative scope for growth. This is the basis for the use of condition index as a measure of health in oysters (e.g. Newell, 1985; Wright and Hetzel, 1985). To allow for this, equation 2 must be modified as

$$\frac{dO_j}{dt} = P_{gj} + P_{rj} + (\text{gain from } j-1) - (\text{loss to } j+1) + (\text{gain from } j+1) - (\text{loss to } j-1) \quad (3)$$

for j = 1,10. The last two terms on the right side of Equation 3 represent the individuals losing biomass and, thus, translating down to the next lower size class.

The relationships used to parameterize the processes in Equation 3 are described in the following sections. More details and a discussion of the assumptions and supporting data for the model were presented by Klinck et al. (1992), Powell et al. (1992) and Hofmann et al. (1992). Accordingly, the basic oyster size class model is outlined only briefly. However, calculations of spawning size and recruitment, mortality, and the effect of oyster density on feeding are specific to this study and are described in more detail.

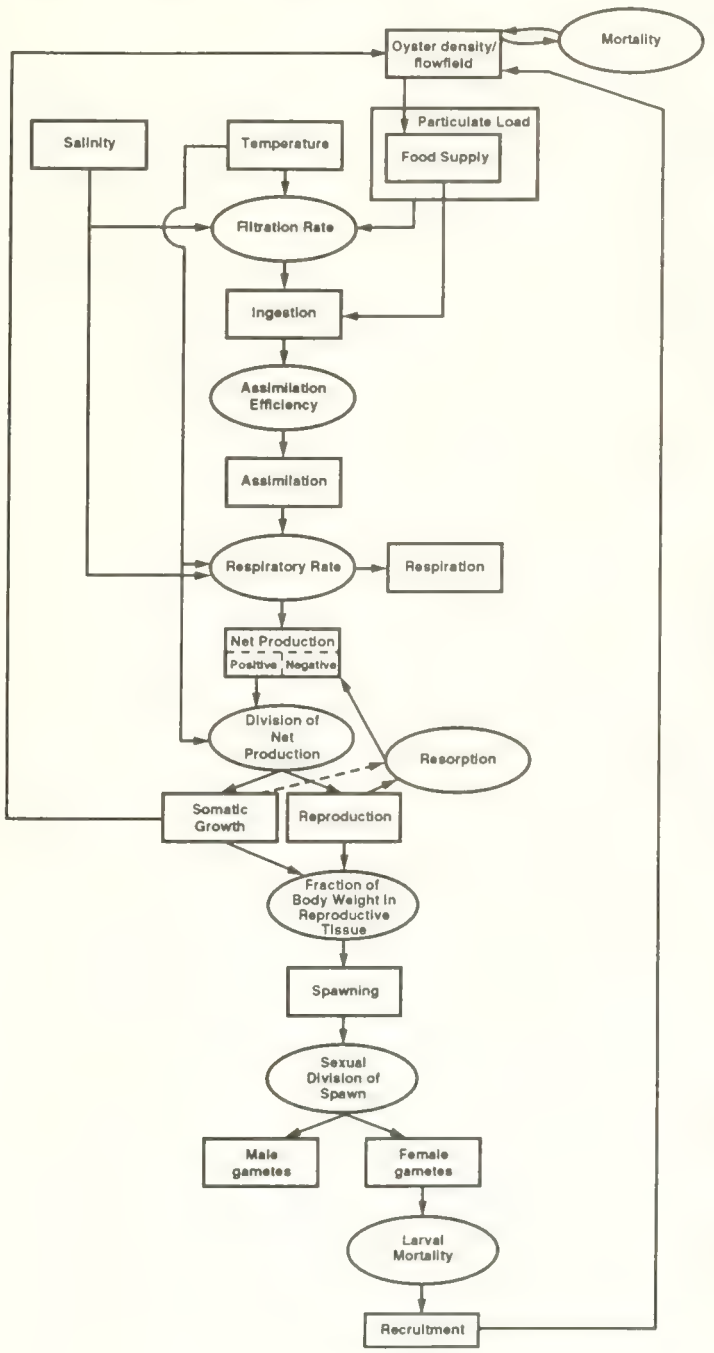


Figure 1
Schematic diagram of the energy flow model.

Feeding and assimilation

Ingestion rate depends upon the filtration rate and the ambient food concentration. We adapted Doering and Oviatt's (1986) equa-

tion for filtration rate to oysters (Powell et al., 1992) to obtain filtration rate as a function of biomass and temperature (T):

$$FR_j = \frac{K_j^{0.96} T^{0.95}}{2.95}, \tag{4}$$

and

$$K_j = W_j^{0.317} 10^{0.669}, \tag{5}$$

where filtration rate (FR_j) is in mL filtered ind^{-1} min^{-1} and W_j is the ash-free dry weight in g for each size class. Equation 4 contains the temperature-dependency described by Loosanoff (1958).

Filtration rate was further modified by salinity as described by Loosanoff (1958). Filtration rate decreases as salinity drops below 7.5‰ and ceases at 3.5‰. In mathematical terms:

$$\begin{array}{ll} \text{at } S \geq 7.5‰ & FR_{sj} = FR_j \\ \text{at } 3.5 < S < 7.5‰ & FR_{sj} = FR_j (S - 3.5)/4.0 \\ \text{at } S \leq 3.5‰ & FR_{sj} = 0. \end{array} \tag{6}$$

where S is ambient salinity and FR_j is the filtration rate obtained from Equation 4.

The reduction in feeding efficiency at high particulate loads was included as a reduction in filtration rate according to Loosanoff and Tommers (1948)

$$\tau = (4.17 \times 10^{-4})(10^{0.0418x}), \tag{7}$$

where τ is the total particulate content (inorganic + organic) in $g \cdot L^{-1}$ and x is the percent reduction in filtration rate.

Solving Equation 7 for the percent reduction in filtration rate gives a modified expression for filtration rate of the form:

$$FR_{\tau j} = FR_{sj}\left[1 - 0.01\left(\frac{\log_{10}\tau + 3.38}{0.0418}\right)\right]. \tag{8}$$

Equation 8, if applied to total particulate content (inorganic + organic), limits ingestion rate to approximately the maximum value found by Epifanio and Ewart (1977). Therefore, an additional term to lower ingestion efficiency at high food concentrations was not used.

The effect of oyster density on food availability was parameterized from measurements given in Lund (1957) as

$$f = \frac{k}{\left[k - f_0 - 1\right] e^{-rd} + 1}, \tag{9}$$

where f is the fractional reduction in food, d is oyster density expressed as L filtered $hr^{-1} \cdot m^{-2}$, and f_0=0.001, an arbitrarily low number conforming to the expectation that food supply is not affected by low oyster density. For the high flow (59 L hr^{-1}) conditions given in Lund (1957), k = 0.31 and r = 1.36×10^{-6}. For low flow (12 L hr^{-1}) conditions, k = 0.57 and $r = 9.746 \times 10^{-7}$. Food availability at a given oyster density is estimated as $(1-f)$ times the ambient food concentration. Filtration rate times the ambient available food concentration then gives oyster ingestion. Assimilation is obtained from ingestion using an assimilation efficiency of 0.75 (Powell et al., 1992).

Respiration

Oyster respiration as a function of temperature and oyster weight was obtained from Dame (1972) as

$$R_j = (69.7 + 12.6T) W_j^{b-1}, \tag{10}$$

where R_j is in µL O_2 consumed $hr^{-1} \cdot g$ dry wt^{-1} and b = 0.75.

Salinity effects on oyster respiration were parameterized from data given in Shumway and Koehn (1982) by obtaining a ratio (R_r) of respiration at 10‰ to respiration at 20‰,

$R_r = \frac{R_{10‰}}{R_{20‰}}$, and regressing this ratio against temperature. This yielded two equations:

$$\begin{array}{ll} \text{at } T < 20°C & R_r = 0.007T + 2.099; \\ \text{at } T \geq 20°C & R_r = 0.0915T + 1.324; \end{array} \tag{11}$$

which were then used to obtain respiration rate as follows:

$$\begin{array}{ll} S > 15‰ & R_{Tj} = R_j; \\ 10‰ < S < 15‰ & R_{Tj} = R_j\left(1 + \left[(15 - S)(R_r - 1)/5\right]\right); \\ S \leq 10‰ & R_{Tj} = R_j R_r. \end{array} \tag{12}$$

Shumway and Koehn (1982) identified effects of salinity on respiration at 20‰; however, we used a 15‰ cutoff to conform to Chanley's (1958) observations on oyster growth.

Reproduction

For adult oysters (j=4,10), net production was apportioned into growth and reproduction by using a temperature-dependent reproduction efficiency of the form

$$R_{effj} = 0.054T - 0.729 \tag{13}$$

for January to June and

$$R_{effj} = 0.047T - 0.809 \quad (14)$$

for July to December. Equations 13 and 14 were derived empirically from the field observations of Soniat and Ray (1985) and may not hold north of Delaware Bay (Hofmann et al., in press).

The portion of net productivity going into reproduction is given by

$$P_{rj} = R_{effj} NP_j, \text{ for } j = 4,10. \quad (15)$$

Somatic growth is the remaining fraction. In cases where $NP_j < 0$, we assume preferential resorption of gonadal tissue to cover the debt. For juveniles and adults with no gonadal tissue, resorption of somatic tissue occurs. We assume that reduced reproduction at low salinity (Engle, 1947; Butler, 1949) results from decreased filtration rate and increased respiratory rate and so include no specific relationship for this effect.

Spawning of the oyster population occurs when the total cumulative reproductive biomass of the population exceeds 20% of the total oyster biomass (Choi et al., 1993). This value is lower than the estimates of Galtsoff (1964) and Deslous-Paoli and Heral (1988), but comes from direct measurements of egg content. Once spawning occurs, the total reproductive biomass is apportioned into male and female biomass according to Kennedy (1982)

$$f_{ratio} = 0.021L_b - 0.62. \quad (16)$$

where f_{ratio} is the ratio of females to males and L_b is shell length in mm obtained from biomass (White et al., 1988). Oysters can change their sex, and Kennedy (1982) suggested that the ratio of males to females is affected by oyster density, salinity, and stress. While perhaps important in some situations, no data exist to parameterize these relationships adequately. They are not included in the model.

The female portion of reproductive biomass (R_f) is converted into eggs spawned by

$$\text{Number of eggs spawned} = R_f \ 1/6133 \ 1/W_{egg} \quad (17)$$

where 6133 is the egg's caloric content (cal g dry wt^{-1}) (Klinck et al., 1992) and W_{egg} is egg weight obtained from

$$W_{egg} = 2.14 \times 10^{-14} V_{egg}, \quad 18$$

where oyster egg volume (V_{egg}) is from Gallager and Mann (1986). The factor 2.14×10^{-14} represents conversions for density, dry wt to wet wt, and μm^3 to cm^3. The egg weight, 13 ng dry wt, calculated from Equation 18 is close to experimentally determined egg weights (Lee and Heffernan, 1991; Choi et al., 1993).

Larval recruitment and mortality

Larval growth rate, which determines the time spent in the plankton, is controlled by ambient food concentration, temperature, salinity, and turbidity. Therefore, larval life span can range from twenty to sixty days (Dekshenieks et al., in press). For the purposes of this modeling study, larval life span was assumed to be twenty days, which may be an underestimate for some environmental conditions, but is in general agreement with observations (Prytherch, 1929; Dupuy et al., 1977; Bahr and Lanier, 1981). We allow an additional 10 days for the larvae to grow to the mean biomass represented by size class one in the post-settlement model. Thus, thirty days after spawning, larvae appear in the simulated post-settlement oyster population as new recruits to the first size class (j=1).

While in the plankton, oyster larvae undergo considerable mortality from a variety of sources. Larval mortality is included in the model by using a simple linear relationship of the form

$$\text{Number of larvae recruited spawn}^{-1} = s(\text{Number of eggs spawned}) \quad (20)$$

where s determines the rate at which individuals are lost per spawn (in spawn^{-1}). No attempt is made to differentiate among sources of oyster larval mortality.

Post-settlement population mortality

Post-settlement oyster populations undergo natural mortality from diseases and predators and man-induced mortality through fishing. Both natural and man-induced mortality vary with season and size of individual. Adult mortality was modeled by using a linear mortality relationship of the form

$$\text{Number dying time}^{-1} = k_d \ (\text{Number living}), \text{ for } j = k,l \quad (21)$$

where k_d determines the daily mortality rate (in day^{-1}) and k and l are the inclusive size classes being affected by mortality. As with larval mortality, this approach does not differentiate among the many sources of oyster mortality. However, the ef-

fect of these mortality sources is implicit in the value chosen for k_d and the size class range used (k,l).

Environmental forcing

Monthly-averaged time series of temperature measured in Galveston Bay (Soniat and Ray, 1985) and Chesapeake Bay (Galtsoff et al., 1947) were used as input to the model (Fig. 2). Each time series is two years in length and each shows temperature trends expected for mid-latitude temperate bays: cool in fall and spring and warm in summer. For a 6-year simulation, the 2-year time series shown in Figure 2 was repeated three times. Salinity values were held constant throughout the year at 24‰ to simplify the discrimination between salinity and temperature effects.

Monthly-averaged values of food concentration were also input into the model (Fig. 2). However, unlike the temperature time series, idealized time series, constructed to illustrate particular types of food availability, were used. This approach was used so that the occurrence and magnitude of features such as the spring and fall phytoplankton blooms could be manipulated (Fig. 2, A and C) or eliminated (Fig. 2B). However, the general characteristics of the idealized food time series are representative of measured values (Soniat et al., 1984; Berg and Newell, 1986). The basic idealized food time series consisted of low winter levels (0.5 $mg \cdot L^{-1}$), higher summer levels (0.75 $mg \cdot L^{-1}$) and still higher values for two months in the spring and fall to simulate spring and fall bloom levels (1.25 $mg \cdot L^{-1}$). A summary of the environmental conditions used for each simulation is given in Table 2.

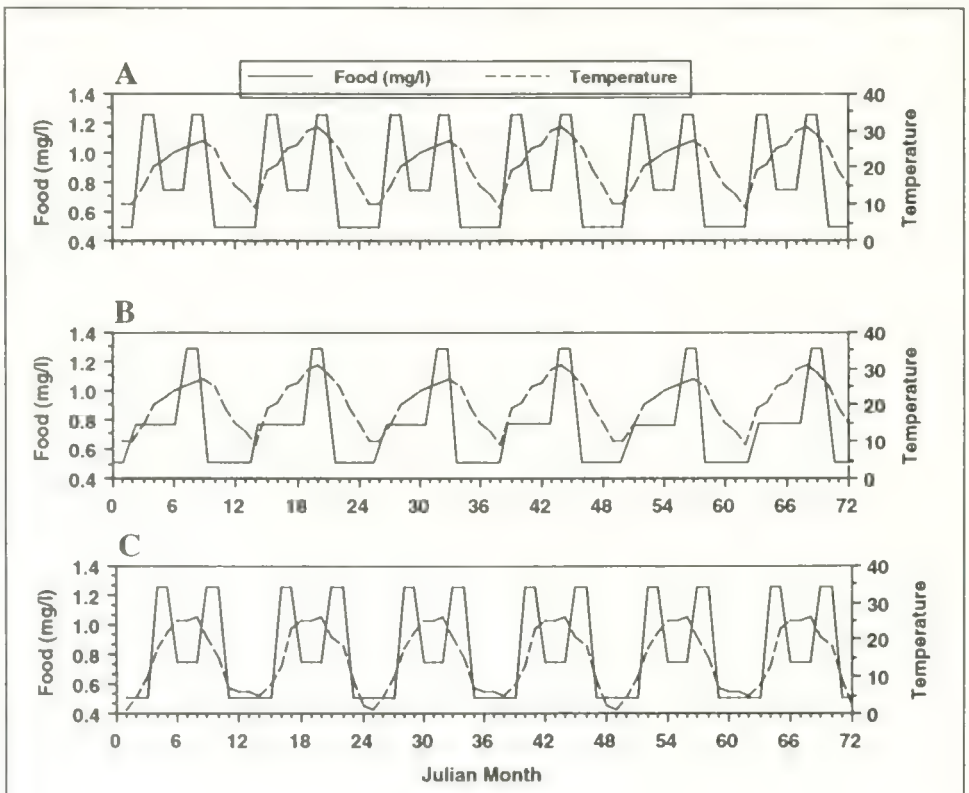


Figure 2

Monthly-averaged time series of temperature and food concentration used as environmental forcing for the oyster population model. (**A**) Temperatures from Galveston Bay (Soniat and Ray, 1985) and plankton biomass for years having blooms in March–April and August–September. (**B**) Temperatures from Galveston Bay and plankton biomass for years having one bloom in August-September. (**C**) Temperatures from Chesapeake Bay with plankton biomass for years having blooms in April-May and September-October. See Table 2 for a description of the food time series used.

Table 2

Summary of environmental and biological conditions used for the oyster *Crassostrea virginica* population simulations. The figure (F) or table (T) displaying the results of each simulation is indicated. All simulations were run using a constant salinity of 24‰, no turbidity, and low flow conditions characteristic of sheltered reefs. An appropriate seasonal time series for temperature was used for Galveston Bay (GB) or Chesapeake Bay (CB) as required (Fig. 2). Three initial densities were used. The numbers per size class for the 10 size classes at these densities are:

low (L):	0	0	0	0	0	0	10	0	0	0
medium (M):	0.1	1.5	5.1	9.2	13.3	5.6	1.4	0.1	0	0
high (H):	490	2240	3637	3217	2502	289	6	0	0	0

A series of standardized food time series was used as depicted in Figure 2. These consisted of 5 winter months at 0.5 $mg \cdot L^{-1}$, 3 or 5 summer months at 0.75 $mg \cdot L^{-1}$ and 2 or 4 bloom months in the spring and/or fall of 1.25 $mg \cdot L^{-1}$. Blooms were of 2-month duration. When two blooms occurred, the two 2-month blooms were separated by 3 summer months. When one 2-month bloom occurred, the bloom was preceded or succeeded by 5 summer months. Table designations are: A/S, August–September bloom; M/A-A/S, March–April and August–September blooms; A/M-S/O, April–May and September–October blooms. Mortality was expressed as a yearly rate: a rate of 99% for instance would have removed 99% of the biomass in one year if no recruitment or growth occurred. For yearly (Y) mortality, this rate was applied for the entire year. For summer (S) mortality, this yearly rate was applied only to the months of April through September. For winter (W) mortality, the yearly rate was applied only to the months of October through March. Recruitment was the fraction of eggs spawned that successfully recruited to the population. In each case, the lowest size class suffering mortality is given (e.g. 5). In every case, all larger size classes also suffered mortality at the same yearly rate: all smaller size classes were unaffected. All simulations began on Julian day 1 (January 1) and were run for 6 years.

Case	Table or figure	Bay	Food time series	Fraction of spawn recruited	Yearly mortality rate	Season of mortality	Size class suffering mortality	Beginning density (day 1)
1	F-3	GB	M/A-A/S	10^{-7}	NA	NA	NA	L
2	F-4,T-2	GB	M/A-A/S	10^{-7}	50%	Y	≥5	H
3	T-2	GB	M/A-A/S	10^{-7}	75%	Y	≥5	H
4	T-2,3,4	GB	M/A-A/S	10^{-7}	90%	Y	≥5	H
5	T-2	GB	M/A-A/S	10^{-7}	99%	Y	≥5	H
6	F-5,T-2,3,4	GB	M/A-A/S	10^{-7}	99.9%	Y	≥5	H
7	T-3	GB	M/A-A/S	10^{-7}	90%	Y	≥3	H
8	F-6	GB	M/A-A/S	10^{-7}	99%	Y	≥3	H
9	F-7,T-3	GB	M/A-A/S	10^{-7}	99.9%	Y	≥3	H
10	F-8	GB	M/A-A/S	10^{-7}	99%	Y	≥1	H
11	F-10e,T-3,4	GB	A/S	10^{-7}	90%	Y	≥5	H
12	F-10f,T-3,4	GB	A/S	10^{-7}	99.9%	Y	≥5	H
13	T-3,4	GB	A/S	10^{-7}	90%	Y	≥3	H
14	F-9,T-3	GB	A/S	10^{-7}	99.9%	Y	≥3	H
15	T-4	GB	A/S	10^{-8}	90%	Y	≥3	H
16	F-10g	GB	A/S	10^{-8}	75%	Y	≥3	H
17	F-10h	GB	A/S	10^{-8}	50%	Y	≥3	H
18	F-10a	GB	A/S	10^{-8}	75%	Y	≥5	H
19	F-10b,T-4	GB	A/S	10^{-8}	90%	Y	≥5	H
20	F-10c	GB	A/S	10^{-8}	99%	Y	≥5	H
21	F-10d,T-4	GB	A/S	10^{-8}	99.9%	Y	≥5	H
22	T-4	GB	M/A-A/S	10^{-8}	99.9%	Y	≥5	H
23	T-4	GB	M/A-A/S	10^{-8}	90%	Y	≥5	H
24	F-11,13,T-5	GB	M/A-A/S	10^{-8}	99.9%	W	>5	H
25	T-5,6	GB	M/A-A/S	10^{-8}	99%	W	>5	H
26	T-5	GB	M/A-A/S	10^{-8}	90%	W	≥5	H
27	T-5	GB	M/A-A/S	10^{-8}	90%	S	>5	H
28	T-5,6	GB	M/A-A/S	10^{-8}	99%	S	>5	H
29	F-12,13,T-5	GB	M/A-A/S	10^{-8}	99.9%	S	>5	H
30	T-5,6	GB	M/A-A/S	10^{-8}	90%	S	≥3	H
31	F-14,T-5	GB	M/A-A/S	10^{-8}	99%	S	>3	H

Table 2 (Continued)

Case	Table or figure	Bay	Food time series	Fraction of spawn recruited	Yearly mortality rate	Season of mortality	Size class suffering mortality	Beginning density (day 1)
32	F-14,T-5	GB	M/A-A/S	10^{-8}	99%	W	≥3	H
33	T-5,6	GB	M/A-A/S	10^{-8}	90%	W	≥3	H
34	F-17,18	GB	M/A-A/S	10^{-8}	99%	S	≥5	M
35	F-17,18	GB	M/A-A/S	10^{-8}	99%	W	≥5	M
36	F-17,18	GB	M/A-A/S	10^{-8}	99%	S	≥6	M
37	F-17,18	GB	M/A-A/S	10^{-8}	99%	W	≥6	M
38	F-17,18	GB	M/A-A/S	10^{-8}	99%	S	≥7	M
39	F-17,18	GB	M/A-A/S	10^{-8}	99%	W	≥7	M
40	T-5	GB	A/M-S/O	10^{-8}	99.9%	W	≥5	H
41	F-15,16,T-5	GB	A/M-S/O	10^{-8}	99.9%	S	≥5	H
42	T-5	GB	A/M-S/O	10^{-8}	90%	W	≥3	H
43	T-5,6	GB	A/M-S/O	10^{-8}	90%	S	≥3	H
44	F-19,20	CB	A/M-S/O	10^{-8}	99%	S	≥5	H
45	T-6	CB	A/M-S/O	10^{-8}	90%	S	≥3	H
46	T-6	CB	M/A-A/S	10^{-8}	90%	S	≥3	H
47	T-6	CB	M/A-A/S	10^{-8}	99%	S	≥5	H
48	F-21,T-6	CB	M/A-A/S	10^{-8}	99%	W	≥5	H
49	T-6	CB	M/A-A/S	10^{-8}	90%	W	≥3	H
50	T-6	CB	A/M-S/O	10^{-8}	90%	W	≥3	H
51	F-20	CB	A/M-S/O	10^{-8}	99%	W	≥5	H

Model solution

The model described by Equation 3 was solved numerically by using an implicit (Crank-Nicolson) tridiagonal solution technique. The time step for model integration was one day. Simulations were run for six years which is sufficient time for the model solutions to adjust so that trends in population levels could be identified in the simulations.

Results

Model initialization

The system of equations given by Equation 3 requires that an initial oyster population size-frequency distribution be specified. The simulations described in the following sections are designed to investigate seasonal and latitudinal mortality effects on oyster population size frequency and stability. Therefore, it proved useful to begin the simulations with a size-frequency distribution representative of a crowded population; that is, one suffering little mortality. In this way, changes in the simulated oyster populations will be the result of mortality only. Also, using the same initial population distribution allows for comparison between simulations throughout the entire 6-year simulated time period.

The initial oyster size-frequency distribution was obtained from a simulation that was started with 10 individuals·m^{-2} in size-class 7 on 1 January. The food time series for this simulation contained two phytoplankton blooms of two months duration (March/April, August/September) with intervening summer months and winter months as detailed in Figure 2. Dense bivalve populations can deplete the surrounding water column of food (Fréchette et al., 1991). We used Lund's (1957) low flow conditions to simulate the effect of oyster density on food supply. Such conditions might be typical of an enclosed or sheltered reef (Powell et al., 1987). No mortality was allowed in any size class.

The time development of the simulated population (Fig. 3A) shows that the mean size of the population slowly declines from size class 7 to size class 3, as population density increases about 3 orders of magnitude. These trends are characteristic of a crowded population: high population density and reduced adult size. Reproduction continues throughout the simulation (Fig. 3, A and C) with a strong fall spawning pulse (Fig. 3B) occurring in response to the fall phytoplankton bloom (Hofmann et al., 1992). Therefore, food limitation is not sufficient to cap population growth; however, the rate of population increase has dramatically declined over the 6-year simulation. It is the population size-frequency distribution at the end of the 6-year simulation (Fig. 3D) that is used to initialize the mortality simulations described in the following sections.

Effect of continuous mortality

The first set of simulations considered the oyster population that would be produced in Galveston Bay, Texas, when continuous mortality (mortality throughout the year) is imposed on size classes 5 and larger. Oyster size class 5 approximates the 2.5 in size limit often desired by the oyster fishery as opposed to the standard size limit of 3 now enforced in most areas. Over this series of simulations, the rate of yearly mortality was varied from 50% to 99.9%, the two extremes being depicted in Figures 4 and 5. For an oyster population with no recruitment, these rates would result in a reduction of the population by 0.5 and 0.999, respectively, in one year. In our simulations, where recruitment and mortality constantly change population abundance, a 50% mortality rate does not necessarily result in the loss of one-half of the individuals in the population in one year.

Over this series of simulations (Table 3, Figs. 4 and 5), as mortality rate increases from 50% to 99.9%, density declines by about 80% and the size-frequency distribution shifts slightly to lower size classes. Population reproductive effort declines as the number of adults declines, but individual reproductive effort increases. At the lower mortality rate, spawning is primarily confined to a single strong pulse in the fall. At the higher mortality rate, spawning effort is distributed between a spring and fall spawning peak; the fall peak is stronger and extends over a longer time (Fig. 4A vs. Fig. 5A).

Moreover, spawning is higher in every other year (Figs. 4C and 5C). In the temperature time series for Galveston Bay (Fig.

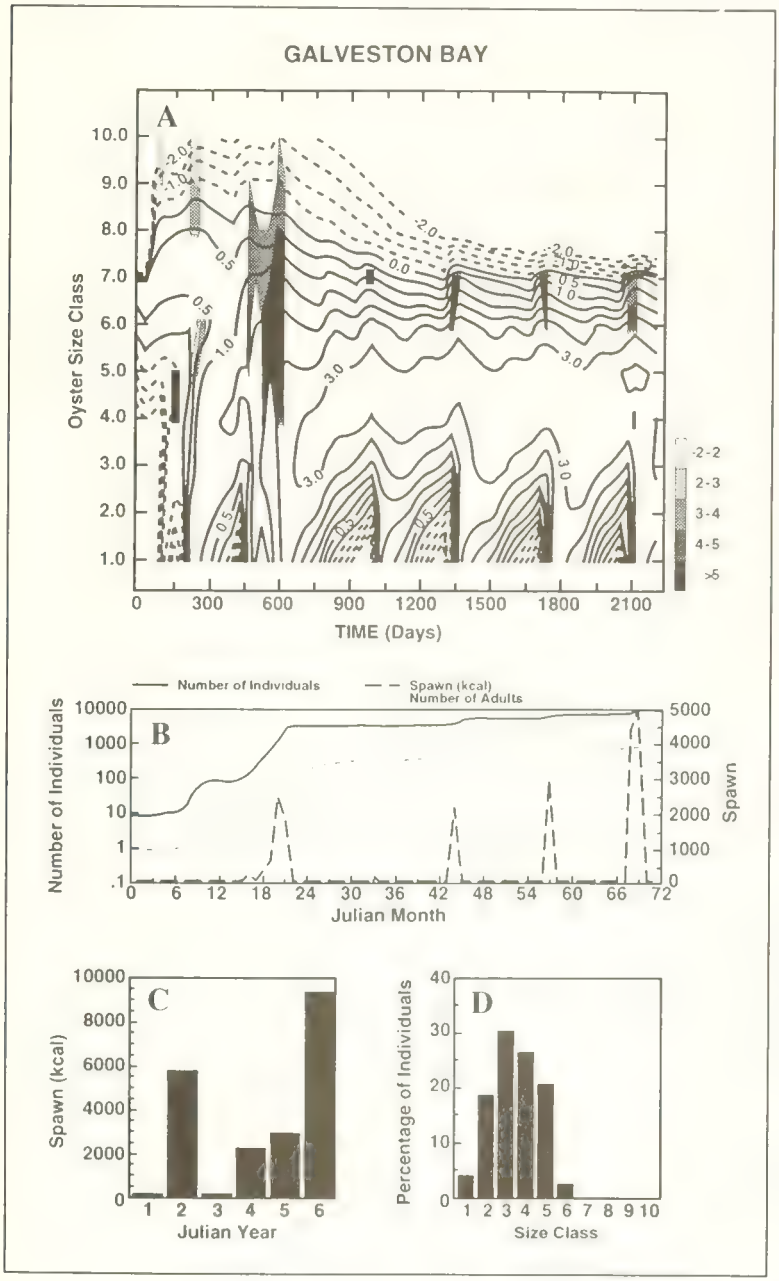


Figure 3

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population with no mortality, allowing the population to approach the carrying capacity of the environment. (**A**) The number of individuals per size class and reproductive effort per size class. Values are plotted opposite the size class designation, not halfway between; hence all individuals in size class 7 are opposite the grid mark labeled 7 on day 1 of this simulation. Isolines, for number of individuals, are the logarithms of the number of oysters ($\log_{10}$N). Hence, the zero contour corresponds to one individual. Population concentrations less than this are indicated by dashed lines; population concentrations greater than this by solid lines. Shading for the amount of reproductive effort (spawn) represents the logarithm of cal ($\log_{10}$cal) with the darkest shades corresponding to highest values. Contour interval is 0.5 for the number of individuals and 1.0 for reproductive effort. (**B**) Monthly-averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. Values can be converted into joules by multiplying by 4.16 j·cal^{-1}; into biomass by using 6100 cal·g dry wt^{-1}; and into the equivalent number of fully developed eggs by 13 ng·egg^{-1} ×6.133×10^{-6} cal·ng^{-1}. (**C**) The yearly reproductive effort (number of kcal spawned). (**D**) The final size class distribution in the population at day 2,160. Additional data and explanation in Table 2, case 1.

2A), one winter is colder and one summer warmer than the other. As a result, the first year in each pair is characterized by lower reproductive effort as decreased temperatures reduce filtration and ingestion rate and switch net production towards somatic growth. Warmer temperatures the second year result in a larger reproductive effort.

Within these simulated oyster populations, a complex interaction exists between population density, size frequency, and mortality rate. Increasing mortality removes individuals, thereby increasing the available food supply for the remaining individuals. Increased food supply results in increased spawning effort, which then increases population density. This in turn then gives reduced spawning effort. This feedback results in potential population equilibria of different densities and size frequencies for each level of mortality (Table 3). Even at 99.9% yearly mortality, however, the population sustains itself at a fairly dense level. Of more significance, each population approaches an equilibrium or nearly so, such that recruitment balances mortality over this range of mortality rates. Year-to-year shifts in population size over the 6-year simulation show neither continually strong declines nor increases in population density for any of the mortality rates.

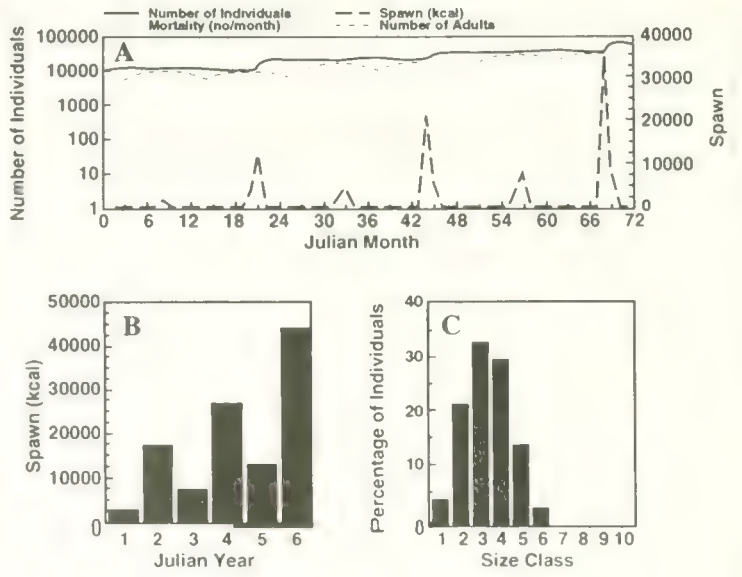


Figure 4

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 50% per year on size classes 5 and larger. (**A**) Monthly averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further explanation in Figure 3 and Table 2, case 2.

In Figures 6–8, we compare the time-development of oyster populations exposed to similar overall mortality levels, but in which mortality extends into lower size classes than in Figures 4 and 5. In these simulations, mortality was imposed either on all adult sizes and the larger juveniles (Figs. 6 and 7) or on all size classes (Fig. 8). Figures 7 and 5 differ only in the size classes exposed to mortality (5 and larger vs. 3 and larger) as do Figures 6 and 8 (3 and larger vs. 1 and larger). As high (90–99.9%) yearly mortality rates are imposed on smaller oyster size classes (Figs. 6–8), the population becomes more susceptible to significant population declines. For example, a 99.9% yearly mortality rate had little effect when mortality was restricted to size classes 5 and larger (Fig. 5), but results in a population crash if size classes 3 and larger are similarly exposed (Fig. 7). Many more individuals die before reproducing in the latter case than in the former. A mortality rate of 99.9% is required for a population crash at size classes 3 and larger (Fig. 7), but only 99% at size class 1 and larger (Fig. 8). As mortality extends into the smaller size classes, the mortality rate that the population can sustain decreases. We note that, although these mortality rates seem high, they are well within the typical range for juvenile survivorship in bivalve communities (e.g. Powell et al., 1984; Cummins et al., 1986).

Table 3

A comparison of final density in simulated *Crassostrea virginica* populations after 6 years and total reproductive effort in year 6 at various rates of yearly mortality. Additional details in Table 2.

Case	Mortality rate (%)	Ending density (day 2160) (ind·m^{-2})	Total reproductive effort in year 6 (kcal·m^{-2})
2	50	50,748	43,158
3	75	16,966	15,093
4	90	33,112	46,426
5	99	12,295	14,211
6	99.9	16,565	19,896

Furthermore, as mortality extends into lower size classes, the size-frequency distribution shifts to larger sizes (Figs. 6C, 7C, 8C). The effect is significant because only in cases where mortality is high do oysters grow large enough to reach marketable size for the oyster fishery (size class 6 and larger). Removal of smaller individuals increases the available food supply for the survivors, thereby allowing some to attain market-size.

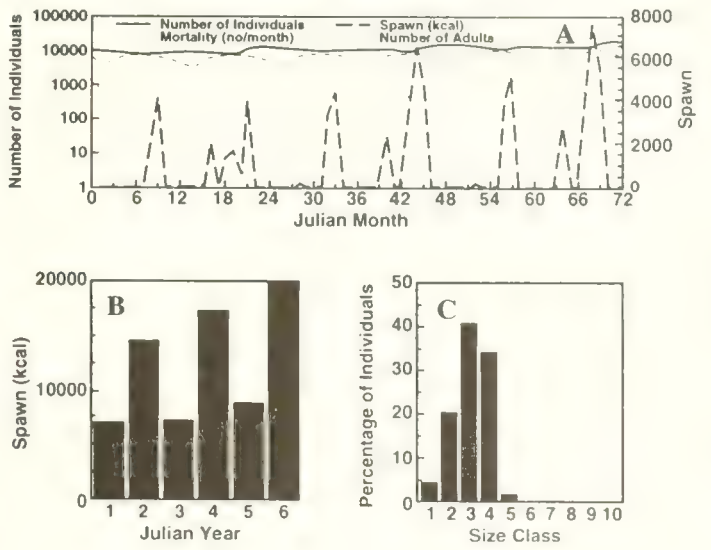
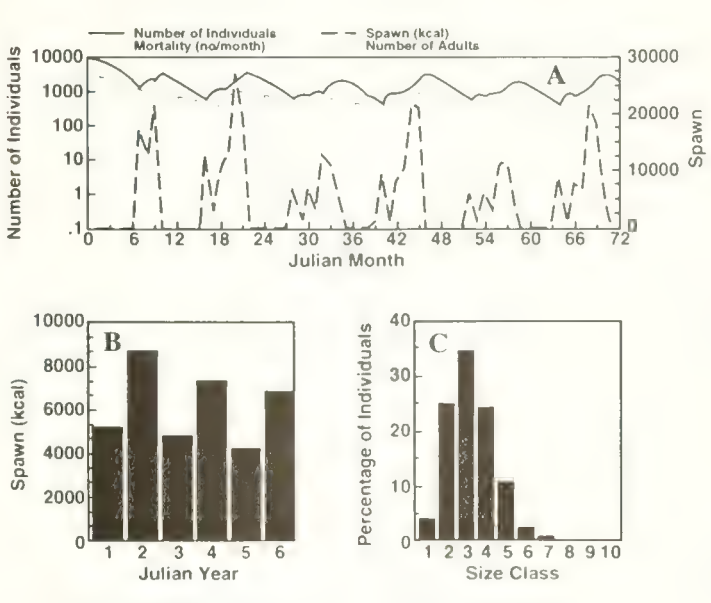


Figure 5

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99.9% per year on size classes 5 and larger. (**A**) Monthly-averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further explanation in Figure 2 and Table 2, case 6.



Effect of food supply

Interactions between food supply and mortality rate are potentially important in determining population density and size-frequency distribution. In years in which a spring bloom is reduced or fails to occur (Fig. 2B), the available food spectrum is shifted in time and total food supply for the year is reduced. In Figure 9, we examine the effect of the failure of the spring bloom. Figure 9 can be compared directly with Figure 7, the two differing only in food supply. A failed spring bloom shifts the food spectrum as well as decreasing the total food available over the year.

Hofmann et al. (1992) showed that the food supply time series used for Figure 9 results in a strong fall spawning pulse. With an imposed yearly mortality of 99.9% in size classes 3 and larger and no spring bloom, the simulated oyster populations (Fig. 9) are not substantially different from those shown in Figures 6–8. However the simulated oyster population shown in Figure 9 is characterized by a stronger fall spawning pulse, as expected, whereas the previous simulations generally had spawning more evenly distributed over the spawning season. The population still reaches a stable distribution and the size-frequency distribution includes individuals in the larger size classes (Fig. 9C). Thus, continuous yearly mortality overrides the effects of variations in the timing of food supply.

Figure 6

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99% per year restricted to size classes 3 and larger. (**A**) Monthly-averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further information in Figure 3 and Table 2, case 8.

However, in this and other simulations, the population density is consistently higher after six years with the lower, more restricted food supply associated with the missing spring bloom (e.g. Fig. 7 vs. 9; Table 4). The effect occurs regardless of the size-class distribution of mortality or the mortality rate. The initial surmise that more food should result in higher densities is not confirmed. Reproductive effort is higher at the higher food supply only in the first year (Fig. 7 vs. 9) and declines more rapidly thereafter as population density declines. Initially this would appear to be counterintuitive; more food should result in higher population densities and greater reproductive effort. However, increased food in the spring increases growth rate so that more oysters grow more rapidly into size classes suffering mortality. As a result, the number of adults and population reproductive potential declines. This results in a lower population density. The model simulations indicate that oyster population abundance is the result of a complicated interplay between the timing of food supply, reproductive effort, and mortality.

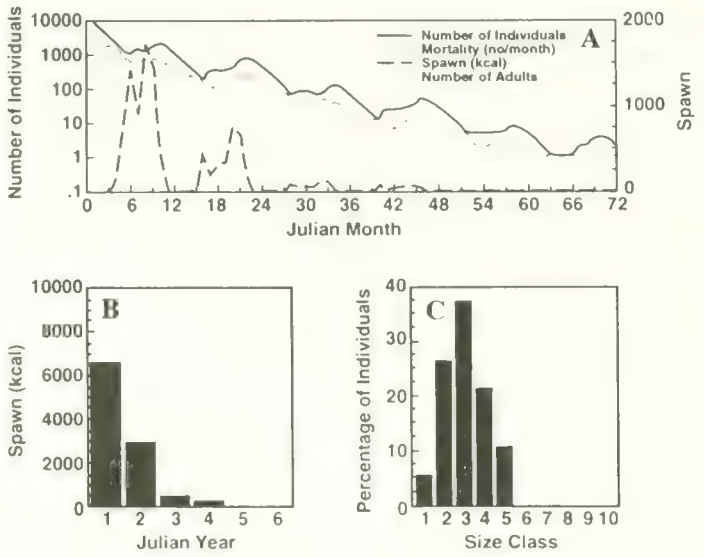


Figure 7

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99.9% restricted to size classes 3 and larger. (**A**) Monthly-averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further information in Figure 3 and Table 2, case 9.

Lowered recruitment success

An additional source of mortality for oyster populations is through decreased survivorship of the planktonic larvae (Table 5, Fig. 10). Lower larval survivorship results in decreased recruitment success and lower population densities, as expected. However, loss of the spring bloom enhances oyster population density as before (Table 5). Nevertheless, a reduction in recruitment success, when combined with mortality on the post-settlement population, results in populations that are less resistant to population crashes. For example, a tenfold reduction in recruitment success in a population exposed to a 75% mortality rate in size classes 3 and larger produces the effect observed for a mortality rate of 99.9% with an order of magnitude higher recruitment success.

One additional important concept arises from this series of simulations. Simulations that included high recruitment success and various mortality rates produced final size-frequency distributions similar to those shown in Fig. 10, E and F. Few individuals are found in size classes 5 and larger. The legal size for the oyster fishery is typically size classes 6 and larger. No fishery could exist under these conditions. High population density produces stunted individuals. A reduction in recruitment success over a range of mortality rates (Fig. 10, A–D) gives size-frequency distributions shifted towards the larger size classes. In fact, more market-sized animals exist in these populations than in the ones shown in Figure 10, E and F. Shifting mortality to lower size classes results in even more market-size individuals (Fig. 10, G–H). A successful fishery requires some degree of mortality, including juvenile mortality.

Effect of seasonal mortality

The commercial oyster fishery is typically confined to a winter season. In some cases, a restricted summer season is also allowed. Agents of natural mortality, like *Perkinsus marinus* and *Thais haemastoma*, typically extract a greater toll during the summer. The effect of mortality restricted to the summer and to the winter is illustrated in Figures 11 and 12, respectively, and in Table 6. For this series of simulations, we define winter as the months of October through March and summer as the months of April through September. Thus each simulated oyster population has the same number

of days (180) with and without mortality. Regardless of the mortality rate, when mortality is restricted to size classes 5 and larger, populations suffer a greater reduction in density when mortality is restricted to the summer (compare Fig. 11B and 12B; Table 6). Summer mortality depresses reproductive effort and depressed reproductive effort, continued over time, results in lower population density.

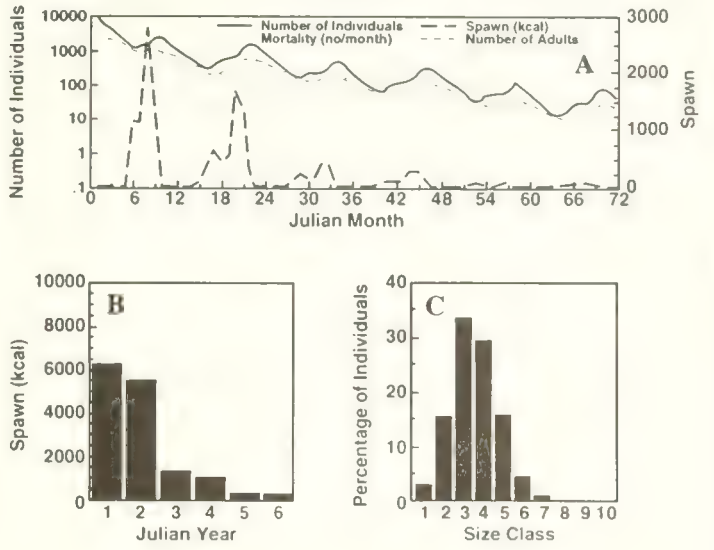


Figure 8

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99% imposed on all size classes. (**A**) Monthly averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further information in Figure 3 and Table 2, case 10.

Examining the population size-frequency distribution over the year for simulated oyster populations suffering winter (Fig. 13, A and B) and summer (Fig. 13, C and D) mortality suggests an explanation for the more detrimental effect of summer mortality on population density. Figure 13 shows snapshots of the population's size-frequency distribution at various times during the year. When mortality is imposed only during the winter, the population size-frequency distribution shifts to larger size classes in the summer in response to increased growth rate produced by warmer temperatures. Therefore, during the fall spawning season the population is dominated by the larger size classes that account for much of the reproductive effort. Winter mortality then shifts the population size-frequency distribution back to smaller individuals (Fig. 13B) and the cycle begins again. Hence, winter mortality allows the population to replace, during the next summer and fall, the individuals that are lost.

In contrast, restricting mortality to summer months produces a population size-frequency distribution that varies little over a year (Fig. 13, C and D). The variation that does occur is a shift towards smaller individuals in the summer. For example, more individuals are found in size classes 6 and 7 in September in populations that experi-

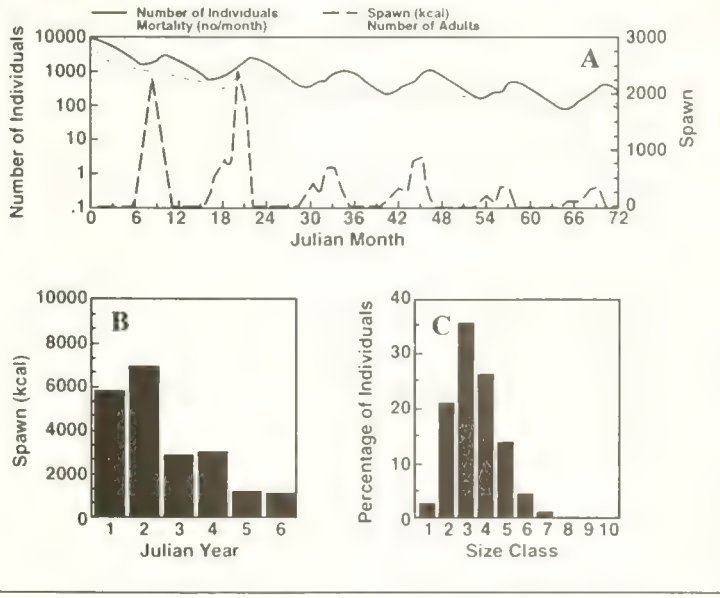


Figure 9

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99.9% restricted to size classes 3 and larger and in which the food time series contained only the fall bloom. The case is comparable to Figure 7 in which two blooms occurred. (**A**) Monthly averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**B**) The yearly reproductive effort (number of kcal spawned). (**C**) The final size class distribution in the population at day 2,160. Further information in Figure 3 and Table 2, case 14.

ence winter (Fig. 13B) rather than summer (Fig. 13D) mortality. The shift to smaller individuals in populations with summer mortality results in lowered reproductive effort. Hence, lost individuals are not replaced in the fall and winter and the population declines.

As mortality extends into the juvenile size classes, the difference in winter and summer mortality should decrease and the seasonal shift in size-frequency as a function of mortality should disappear because a greater fraction of the total mortality occurs in individuals contributing relatively little to the population's spawning potential. This is confirmed by the model (Fig. 14, Table 6). Interestingly, although the seasonal variations in size-frequency distributions are muted, changes in size-frequency distribution over the year are still greater for populations that experience winter mortality. These populations show a slight shift to smaller size classes in the winter.

To examine the effect of varying food supply, we placed the spring and fall blooms one month later in the year (April/May and August/September) and then compared the time development of oyster populations suffering winter or summer mortality with those previously described when the blooms occurred one month earlier (Tables 6 and 7). For populations experiencing winter mortality, delaying the spring and fall blooms by one month (Fig. 2C) does not significantly change the simulated populations from those obtained for the earlier blooms, even when mortality extends to the juvenile size classes (3 and larger). However, for summer mortality, delaying the blooms by one month dramatically improves the population's ability to sustain itself (Fig. 12 vs. Fig. 15; Table 5). Moving the spring and fall blooms one month later in the year produces 1) a strong spring spawning pulse as well as the fall pulse and 2) a shift in the population size-frequency distribution toward the larger size classes, although yearly changes in the size-frequency distribution are still characteristic of summer mortality (Fig. 16 vs. 13). As a result, spawning effort increases under the delayed-bloom condition as fall spawning extends beyond the summer season of mortality. Accordingly, variation in the timing of food supply, under certain circumstances, can be important in the success of an oyster population, particularly in cases where adult mortality is restricted to the summer months.

Table 4

A comparison of final density in simulated *Crassostrea virginica* populations after six years and total reproductive effort in year 6 with and without a spring phytoplankton bloom. Additional details in Table 2.

Case	Spring bloom?	Ending density (day 2,160) ($ind \cdot m^{-2}$)	Total reproductive effort in year 6 ($kcal \cdot m^{-2}$)
9	Yes	2	12
14	No	248	1,003
7	Yes	2,602	7,787
13	No	2,788	7,398
6	Yes	16,565	19,896
12	No	32,513	36,569
4	Yes	33,112	46,426
11	No	42,758	39,217

Table 5

A comparison of final density in simulated *Crassostrea virginica* populations after 6 years and total reproductive effort in year 6 at various rates of recruitment, with and without a spring phytoplankton bloom. Additional details in Table 2.

Case	Mortality rate	Recruitment	Ending density (day 2,160) ($ind \cdot m^{-2}$)	Total reproductive effort in year 6 ($kcal \cdot m^{-2}$)
		No spring bloom		
13	90%	10^{-7}	2,788	7,398
15		10^{-8}	2	26
11	90%	10^{-7}	42,758	39,217
19		10^{-8}	1,067	12,480
12	99%	10^{-7}	32,513	36,569
21		10^{-8}	11	236
		Spring bloom		
6	99%	10^{-7}	16,565	19,896
22		10^{-8}	1	40
4	90%	10^{-7}	33,112	46,426
23		10^{-8}	328	4,935

Size limits for the fishery

Three size limits have been used or considered as the legal limit for market-size oysters: 2.5 in, 3.0 in,

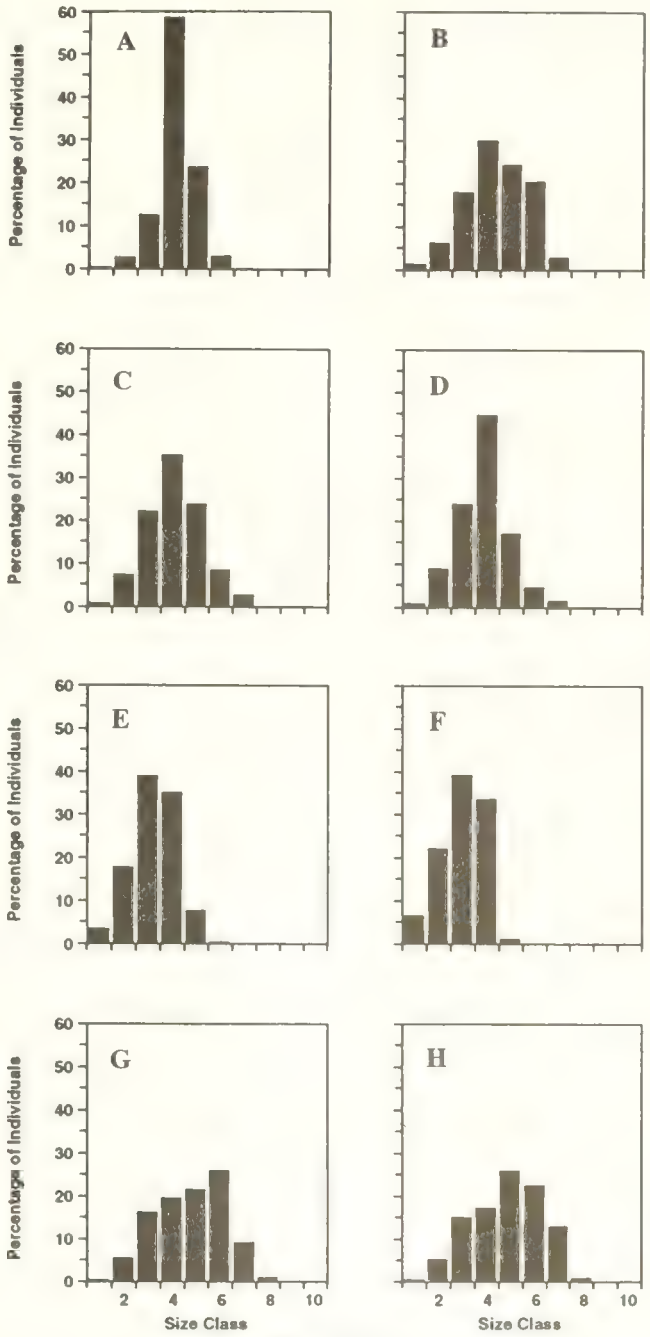


Figure 10

A comparison of the final size-frequency distributions (day 2,160) in simulated *Crassostrea virginica* populations exposed to a Galveston Bay temperature time series following 6 years of recruitment, growth, and mortality under varying degrees of recruitment and mortality. In each case, size classes 5 and larger were exposed to continuous mortality at a yearly rate of (**H**) 50%, (**A** and **G**) 75%, (**B**) 90%, (**C** and **E**) 99%, (**D** and **F**) 99.9%. Recruitment was tenfold higher (or larval mortality tenfold less severe) in E and F. Mortality rates extend down into size classes 3 and 4 in G and H. Further information in Figure 3 and Table 2, cases 11, 12, 16–21.

and 3.5 in. These correspond to size classes 5, 6, and 7 in the model. The simulations used to test the effect of these size limits were initialized with a population size-frequency distribution having a component in the larger size classes (Fig. 12). With a yearly mortality rate of 99%, oyster populations increase when mortality is restricted to size class 7 and larger (3.5 in) but decline rapidly if mortality includes size classes 5 and 6 (2.5 in) (Fig. 17). Hence, a change in the legal size limit may have a substantial effect on the fishery and on the oyster population as a whole. Of course, the specific results would vary according to the biomass-to-length conversion used.

As the fishing season typically is confined to the winter, we examined the effect of changing size limits when mortality was restricted to the winter or to the summer months (Fig. 17). Overall, the same pattern persisted in both seasons. Populations declined more under the smaller size limits. However, several significant differences are also observed:

1 Populations in which mortality was restricted to the summer had a stronger spring spawning pulse; most spawning occurred in the midsummer and early fall in populations suffering only winter mortality.
2 Reproductive effort and population density was consistently higher in populations suffering winter mortality (Fig. 18, C, D, and E), density by a factor of 2 to 4, reproduction by a factor of 2 to 8; increased reproductive effort occurred both because the number of adults increased and because those adults spawned more with the result that reproduction was more than proportionately higher.
3 The size-frequency distribution was shifted toward the smaller size classes in populations having winter mortality (Fig. 18, A and B) but had little impact on the size-frequency distribution with summer mortality.

Overall, the number of market-size oysters available at the end of the simulation was higher at the larger size limits (Fig. 18F). As a result, a greater potential yield was available to the fishery at the larger size limits. One reason for the higher yield available to the fishery at the larger size limit (≥3.5 in) is the shift in size-frequency distribution toward larger size classes with adult mortality. A second reason is the protection of a larger portion of the reproductive population. However, if unchecked, the continually growing population in the last set of simulations, where

Table 6

A comparison of final density in simulated *Crassostrea virginica* populations after six years and total reproductive effort in year 6 with mortality restricted to the winter or the summer season and with the spring and fall phytoplankton blooms early in the year or one month later. Additional details in Table 2.

Case	Season	Ending density (day 2,160) (ind·m^{-2})		Total reproductive effort in year 6 (kcal·m^{-2})	
	Mortality: ≥5	Bloom: Early	Late	Bloom: Early	Late
24, 40	Winter	287	220	5,168	4,344
29, 41	Summer	36	500	606	6,904
25	Winter	467		7,365	
28	Summer	253		3,586	
26	Winter	1,400		4,529	
27	Summer	1,333		13,107	
	Mortality: ≥3				
33, 42	Winter	403	595	5,890	8,664
30, 43	Summer	623	692	7,766	8,829
32	Winter	5		111	
31	Summer	5		91	

Table 7

A comparison of final density in simulated *Crassostrea virginica* populations after six years and total reproductive effort in year 6 with mortality restricted to the winter or the summer season and with the spring and fall phytoplankton blooms early in the year or one month later, in Chesapeake Bay and Galveston Bay. Additional details in Table 2.

Case	Bay	Ending density (day 2,160) (ind·m^{-2})		Total reproductive effort in year 6 (kcal·m^{-2})	
	Mortality: ≥5 Winter	Bloom: Early	Late	Bloom: Early	Late
48	Chesapeake	394		3,924	
25	Galveston	467		7,365	
	Summer				
47	Chesapeake	102		644	
28	Galveston	253		3,586	
	Mortality: ≥3 Summer				
46, 45	Chesapeake	72	85	328	542
30, 43	Galveston	623	692	7,766	8,829
	Winter				
49, 50	Chesapeake	122	84	832	606
33, 42	Galveston	403	595	5,890	8,664

mortality was restricted to size class 7 and larger (≥3.5 in), would eventually negate both effects as population density increased.

Effect of latitude on population stability

In Figure 19 and Table 7, we compare the time-development of oyster populations under the temperature conditions of Chesapeake Bay with those under the temperature conditions of Galveston Bay (Fig. 15). In comparison with the Galveston Bay populations, those in Chesapeake Bay are characterized by densities 2 to 5 times lower, reproductive efforts as much as a factor of 10 lower, size-frequency distributions considerably shifted toward the large size classes (Figs. 20 and 21), and discrete spo-

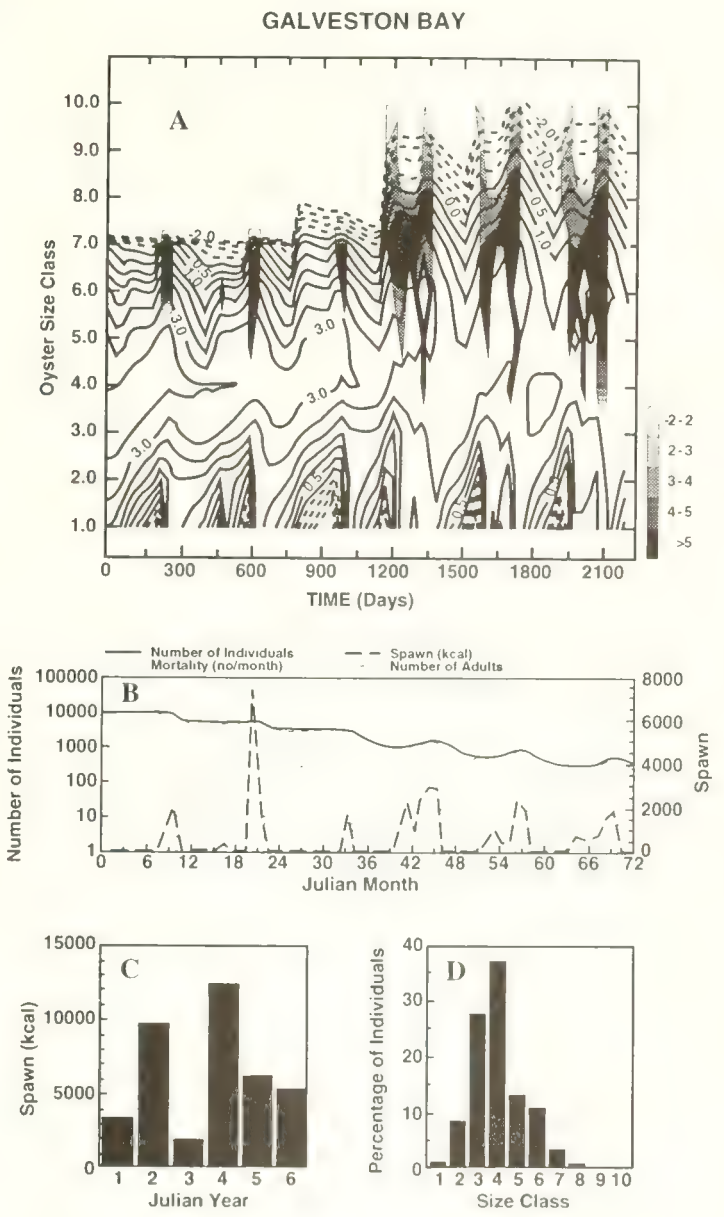


Figure 11

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99.9% restricted to size classes 5 and larger and in which mortality occurred only during the winter. Compare Figure 12. (**A**) The number of individuals per size class and reproductive effort per size class. Isolines, for number of individuals, are the logarithms of the number of oysters ($\log_{10}$N). Shading for the amount of reproductive effort (spawn) represents the logarithm of cal ($\log_{10}$cal). (**B**) Monthly averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**C**) The yearly reproductive effort (number of kcal spawned). (**D**) The final size class distribution in the population at day 2,160. Further information in Figure 3 and Table 2, case 24.

radic spawning pulses typically strongest in midsummer. Like Galveston Bay populations, a shift in the timing of the spring and fall blooms has little effect on the seasonal changes in size-frequency distribution (Fig. 21) but considerable effect on the resulting population density in some cases. Populations experiencing winter mortality are more affected by variations in the timing of the food supply than populations experiencing summer mortality. Unlike Galveston Bay populations, populations experiencing summer mortality have lower population densities than populations experiencing winter mortality only when the blooms occur in March/April and August/September. Delaying the blooms by one month results in little variation between populations experiencing summer and winter mortality. The most significant factor producing differences between the Galveston Bay and Chesapeake Bay populations is the cooler temperatures that characterize Chesapeake Bay. This results in reduced reproductive effort with more net production going to support somatic tissue growth (Table 7).

Discussion

The importance of mortality

Unlike an oyster population, an oyster fishery cannot persist without large adult individuals. One of the consistent messages of this modeling exercise is the requirement of mortality for the population to produce larger, market-size individuals. Either adult or juvenile mortality will suffice, as both juveniles and adults compete for food (Powell et al., 1987). Low rates of mortality result in crowding, food limitation, and a stunted population. As mortality extends into the juvenile size classes, and finally into the larval stages (modeled as a reduction in recruitment, reduced reproductive effort, or produced by the colder temperatures of Chesapeake Bay) the population on the average becomes skewed more and more towards the larger adult size classes. Frequently, this proportional shift was sufficient to result in an increase in adult density despite an overall lower population density. An even higher rate of mortality reversed this trend; the popula-

tion size-frequency shifted again towards smaller size classes as adult individuals were rapidly removed from the population. Clearly, for a successful fishery, a delicate balance exists between sufficient mortality to permit the fishery to exist and too much mortality which will reduce the harvestable yield.

Food supply is a complicating factor. Increased food supply will not always result in increased population density or increased harvestable yield. The timing of the food supply interacts in subtle ways with the timing and intensity of mortality, sometimes producing higher densities and sometimes lower ones. The simulations show that the effect of variations in food supply is complex; no simple rules apply and a number of feedback mechanisms exist. In one case, for example, lower population density resulted from increased food supply because increased growth permitted more oysters to enter the size classes that were exposed to mortality, thereby resulting in a population that declined. In another case, a one-month change in the timing of the spring and fall blooms changed population density by a factor of 2 at the same mortality rate. In other cases, little impact occurred in the population despite, for example, the complete failure of the spring bloom.

Population stability and population crashes

The stability of oyster populations is sensitive to several factors, including the timing and intensity of mortality, latitude, and food supply. (We use the term stable in the sense of Underwood [1989] for populations able to recover quickly from perturbation. The terms elasticity and resiliency might also be used.) Increased mortality reduced population density in every comparison. Oftentimes, a relatively stable equilibrium occurred as recruitment balanced mortality over the long term. In all cases, however, mortality rates sufficient to destabilize this equilibrium could be found and a population decline resulted. When mortality extended over a wider range of size classes or affected larval survivorship, population destabilization occurred more easily. In the former case, more oysters

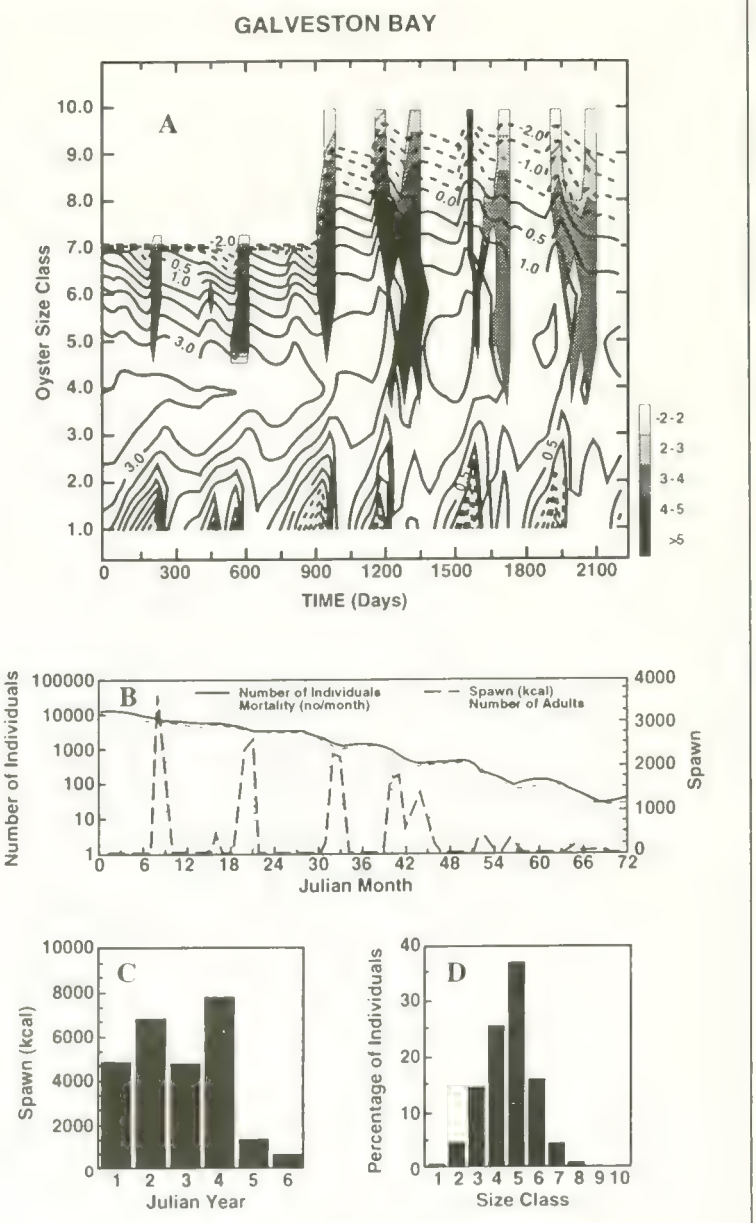


Figure 12

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to a continuous mortality rate of 99.9% restricted to size classes 5 and larger and in which mortality occurred only during the summer. Compare Figure 11. (**A**) The number of individuals per size class and reproductive effort per size class. Isolines, for number of individuals, are the logarithms of the number of oysters ($\log_{10}$N). Shading for the amount of reproductive effort (spawn) represents the logarithm of cal ($\log_{10}$cal). (**B**) Monthly averaged values of the number of individuals, the number of adults (j=4, 10), and the monthly reproductive effort in kcal for the 6-year simulation. (**C**) The yearly reproductive effort (number of kcal spawned). (**D**) The final size class distribution in the population at day 2,160. Further information in Figure 2 and Table 2, case 29.

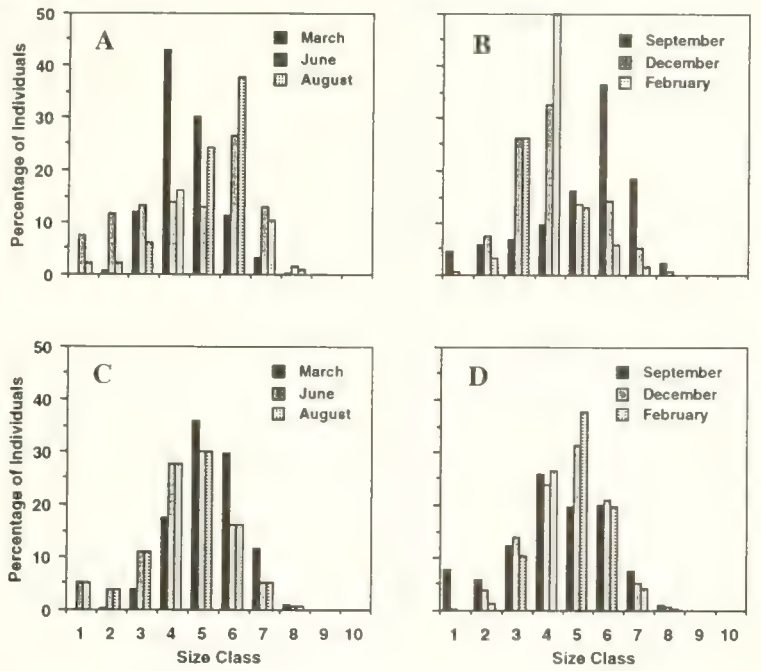
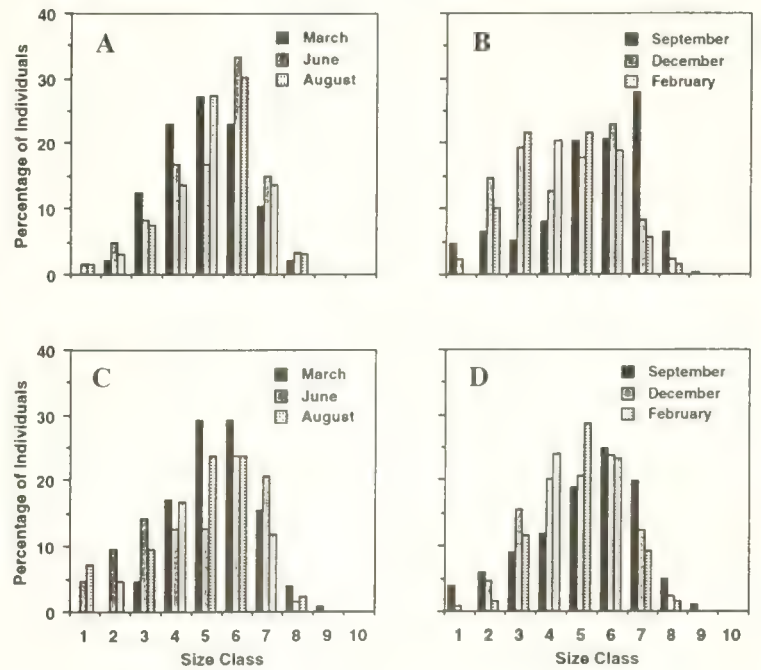


Figure 13

A comparison of the changes in size-frequency distribution through the year in the two *Crassostrea virginica* populations depicted in Figures 11 and 12. (**A** and **B**) a population suffering winter mortality; (**C** and **D**) a population suffering summer mortality. Mortality in both cases was restricted to size classes 5 and larger.



were exposed to mortality. In the latter case, lowered recruitment no longer balanced the higher rates of mortality.

In cases where mortality was imposed for time periods of less than one year, mortality restricted to the six summer months (April–September) nearly always resulted in decreased population density compared to mortality restricted to the winter months. Rarely did the two yield similar results. Never did summer mortality have a lesser impact. The effect was noted at different latitudes, in populations having mortality restricted to a variety of differing size classes, and in populations varying in larval survivorship. However, adult mortality was required. Extending mortality into the juvenile size classes minimized the effect.

Nearly all reports of population crashes in oyster populations result from adult summer mortality, recruitment failure, or floods. Most predators and parasites are most effective in the summer. The series of simulations presented here suggests that the explanation for the importance of adult summer mortality does not necessarily reside in the fact that the most significant agents of adult mortality (except the fishery) operate most effectively in the summer. Although this may well be true, the oyster itself would appear to be more susceptible to mortality in the summer. That is, a greater chance of population crashes in the summer may be physiologically preordained. One potentially important mechanism causing this increased susceptibility is the temperature control on the partitioning of somatic tissue and reproductive tissue in the winter, spring, and summer. Fewer individuals are present in the adult size

Figure 14

A comparison of the changes in size-frequency distribution through the year in simulated *Crassostrea virginica* populations having size classes 3 and larger exposed to mortality. Compare to Figure 13 where mortality was restricted to size classes 5 and larger. (**A** and **B**) mortality restricted to the winter; (**C** and **D**) mortality restricted to the summer. More information in Figure 3 and Table 2, cases 31 and 32.

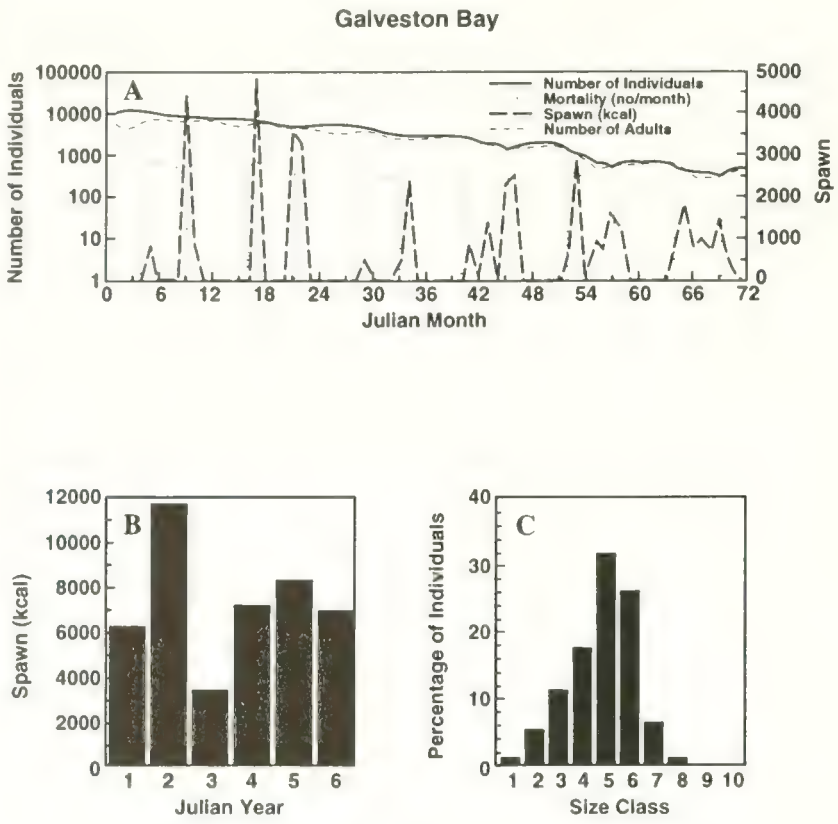


Figure 15

Simulated time development and population distribution of a Galveston Bay *Crassostrea virginica* population exposed to summer mortality at a yearly rate of 99.9% restricted to size classes 5 and larger and in which the food time series contained blooms in April/May and September/October. Figure 12 contains comparable results in which the food time series contained two blooms one month earlier. For additional information, see Figure 3 and Table 2, case 41.

classes in the winter, hence losses are minimized. Juveniles grow rapidly to adulthood in the spring and spawn in the summer. As a result, reproductive effort is higher and population stability is enhanced when mortality is restricted to the winter.

One of the interesting observations from the simulations is the consistent difference in the seasonal shifts in size-frequency distribution exhibited by populations suffering adult summer or winter mortality. Populations impacted most significantly by summer mortality had relatively stable size-frequency distributions over the year. Winter mortality produced strong seasonal shifts in the size-frequency distribution. The results suggest that seasonal shifts in size-frequency distributions might provide a useful measure of the relative importance of summer and winter mortality and of adult mortality in oyster populations. For example, the seasonal cycle in market-sized individuals on some Galveston Bay reefs (e.g. Figure 2.1 in Quast et al., 1988) is similar to the seasonal shifts observed in simulated populations in which mortality was restricted to the winter months, suggesting that the fishery might be an important source of mortality in these populations.

Latitudinal gradient in stability

Although not conclusive, the literature reviewed earlier suggests a latitudinal gradient may exist in oyster population stability. Populations at higher latitudes may be more susceptible to population crashes. The Galveston Bay and Chesapeake Bay simulations support this possibility. Simulated popu-

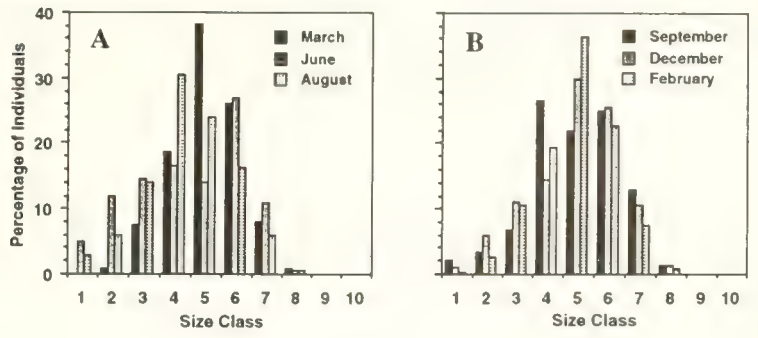


Figure 16

The seasonal changes in size-frequency distribution of the *Crassostrea virginica* population depicted in Figure 15. Figure 13 gives comparable results for the comparable simulation depicted in Figure 12.

lations in Chesapeake Bay were more susceptible to population crashes than those in Galveston Bay. Simulated populations in Galveston Bay consistently had higher population densities after 6 years. Reproductive effort was higher because more of the year occurred within the temperature range conducive to spawning. Higher reproductive effort balanced a larger rate of mortality; hence mortality rates had to be substantially higher in Galveston Bay to effect a population crash. Although not simulated, recovery rates should have been faster as well. Like the distinction between winter and summer mortality, this latitudinal gradient in population stability would appear to result from the basic physiology of the oyster. The fundamental physiological mechanisms associated with reproduction and the division of net production into somatic and reproductive growth would appear to be responsible.

Implications for fisheries management

The methods for managing the *C. virginica* fishery are generally limited to three somewhat interconnected decisions: 1) what size limit should be set; 2) what season should be allowed; and 3) what population density should trigger season closure? The setting of size limits may depend on biological and economic issues. Only biological issues will be considered here. Two aspects of oyster physiology are most important in determining size limits.

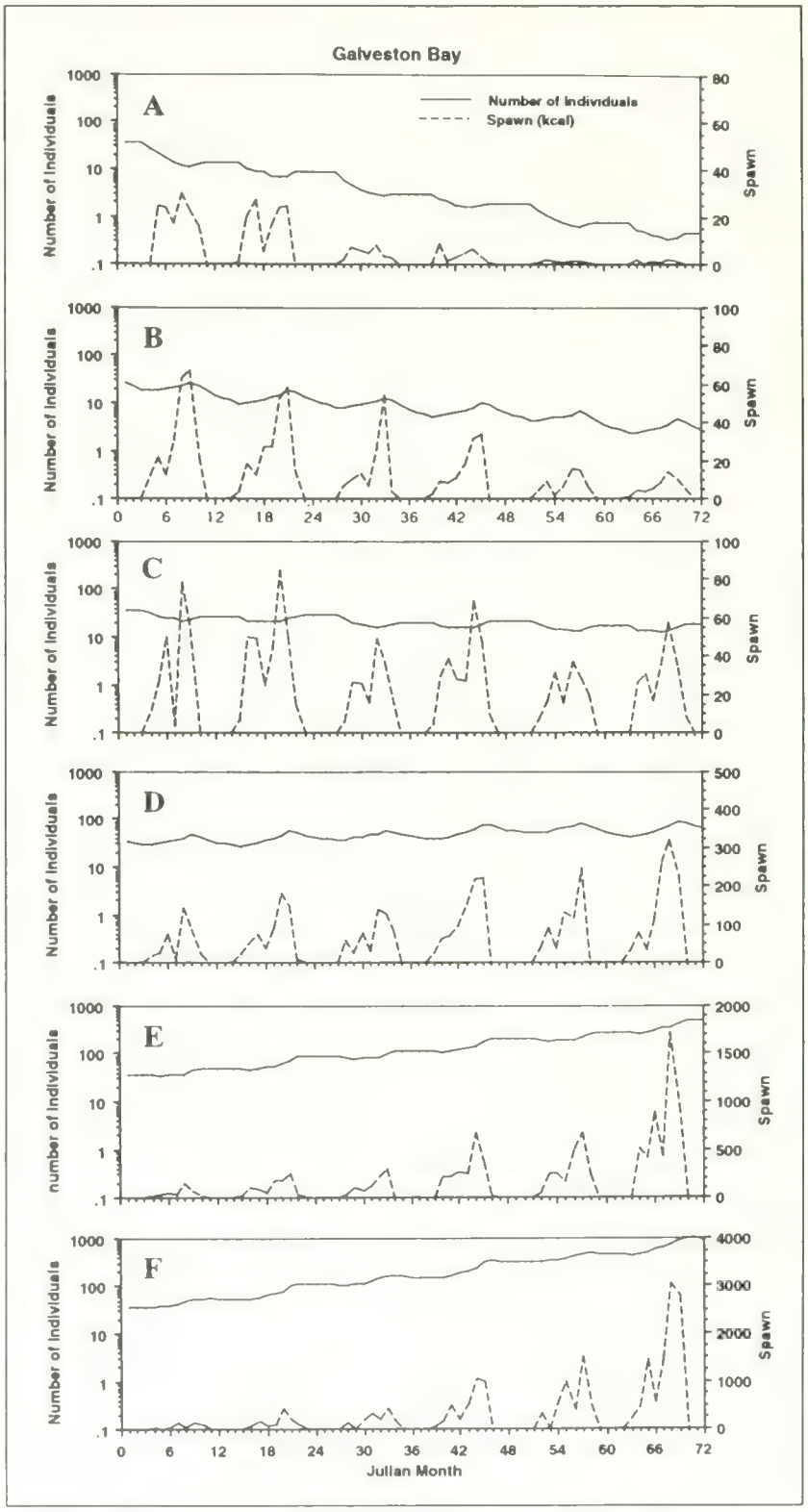
First, under conditions of crowding and at lower latitudes, oysters fail to grow to large size. The former is due to food-limiting conditions. The latter is due to warmer temperatures resulting in the shunting of net production into reproductive growth (Hofmann et al., in press). A considerable body of data supports food limitation in oyster populations, from aspects of spatial distribution (Powell et al., 1987), to reduced growth in crowded locations (Osman et al., 1989), and the observation of increased growth coincident with high mortality (Crosby et al., 1991). A latitudinal gradient in size bespeaks of the importance of temperature in determining the degree to which net production is allocated to somatic growth (Hofmann et al., in press). Both phenomena are reproduced by the model. Clearly, in either case, the setting of size limits as currently done has the effect of artificially reducing yield. If economic considerations warrant it, lower size limits should be set in these populations. In crowded conditions, adult mortality might even increase adult size and yield.

Second, raising size limits increases population density and, under certain conditions, the resulting increase in reproductive effort can eventually result in an increased number of market-size oysters at the larger size limit. Such conditions are met in populations of relatively low density where oysters of legal size are already abundant. Of importance is the recognition that this condition occurs only in populations suffering a relatively high degree of mortality relative to the recruitment rate. Many other agents of mortality, besides the fishery, are important in oyster populations and these agents generally do not respect legal size limits. The model suggests that raising size limits will only be effective if the fishery is the predominant cause of mortality in the population or if other agents of mortality are generally restricted to these same size classes. If all adults are affected, then raising size limits will be ineffective.

Besides the setting of size limits, management policy normally includes a restriction of the fishing season. Fishing seasons on public grounds are generally restricted to the winter months. In some cases, certain areas are set aside for a summer season as well. Natural mortality rates are high in oyster populations, generally greater that 70% per year (Mackin, 1959). Oyster populations in the Gulf of Mexico withstand this degree of mortality without long-term population declines. In this sense, the populations are stable (other species are stable at much higher mortality rates, e.g. Zonneveld [1991]). Rates of recruitment are sufficient to balance mortality over the long term. Nevertheless, population declines do occur (Sindermann, 1968; and others referenced previously) and these have, on occasion,

Figure 17

Comparison of the time development of simulated *Crassostrea virginica* populations exposed to mortality in three differing size classes: (**A** and **B**), sizes 5 and larger; (**C** and **D**) sizes 6 and larger; (**E** and **F**) sizes 7 and larger. Cases A, C, and E show the time development under conditions where mortality was restricted to the summer. Cases B, D, and F show the time development under conditions where mortality was restricted to the winter. Further information in Figure 3 and Table 2, cases 34–39.



been blamed on overfishing. Although no adequate data are available, one suspects that the fishery may be a principle source of mortality in the winter, but not in the summer when the various other agents of mortality, such as diseases and predators, are active.

Oyster populations are more resistant to winter mortality than to summer mortality. The increased likelihood of an intense population decline during the summer observed throughout the oyster's latitudinal range is a product of the basic physiology of the oyster. Simulated oyster populations were most resistant to population declines when mortality was restricted to the winter months under nearly all conditions of recruitment, size-class specific mortality and food supply; they were never less resistant. The simulations suggest that oyster populations can withstand substantially higher rates of mortality in the winter than in the summer and, under conditions where fishing is the primary cause of mortality, populations should be managed more conservatively during the summer season.

A latitudinal gradient in stability exists in oyster populations. Population declines without short-term recovery are more likely at higher latitudes. The simulations suggest that populations should be more and more sensitive to natural agents of mortality and to management decisions at ever increasing latitudes. In effect, populations in the Gulf of Mexico, by their physiology, can withstand the vagaries of nature and the mistakes of man much easier than populations on the Mid-Atlantic and northeast coasts of the United States. The evidence suggests the need for more conservative oyster management at higher latitudes. In effect, the Gulf of Mexico populations and the northeastern

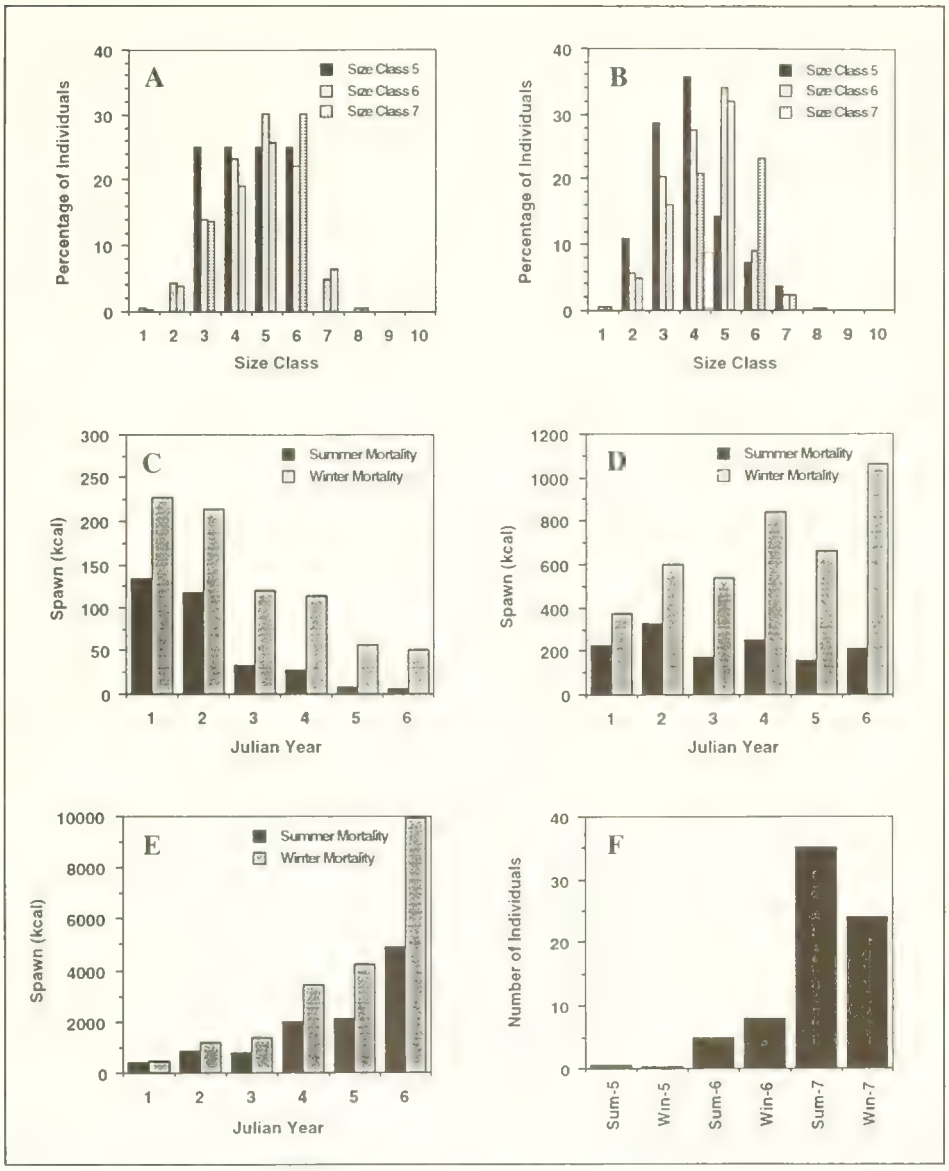


Figure 18

A comparison of the final size-frequency distributions (day 2,160) (**A** and **B**), the yearly reproductive efforts (**C, D,** and **E**) and the number of market-size individuals in the *Crassostrea virginica* population after 6 years (**F**) for the simulations depicted in Figure 17. (A) mortality restricted to the summer (Fig. 17, A, C, and E). (B) mortality restricted to the winter (Fig. 17, B, D, and F). (C) Yearly reproductive effort for populations exposed to mortality in sizes 5 and larger (Fig. 17, A and B). (D) Yearly reproductive effort for populations exposed to mortality in sizes 6 and larger (Fig. 17, C and D). (E) Yearly reproductive effort for populations exposed to mortality in sizes 7 and larger (Fig. 17, E and F). (F) The number of market-size individuals in the population after 6 years, restricting the calculation of market-size individuals to the same classes suffering mortality, 5 and larger (sum-5, Fig. 17A; win-5, Fig. 17B), 6 and larger (sum-6, Fig. 17C; win-6, Fig. 17D) and 7 and larger (sum-7, Fig. 17E; win-7, Fig. 17F).

populations exist under different physiological constraints and these constraints demand different management philosophies and decisions.

Acknowledgments

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Literature cited

Andrews, J. D., D. Haven, and D. B. Quayle.
1959. Fresh-water kill of oysters (*Crassostrea virginica*) in James River, Virginia, 1958. Proc. Natl. Shellfish. Assoc. 49:29–49.

Andrews, J. D., and W. G. Hewatt.
1957. Oyster mortality studies in Virginia. II: The fungus disease caused by *Dermocystidium marinum* in oysters in Chesapeake Bay. Ecol. Monogr. 27:1–26.

Bahr, L. M., and W. P. Lanier.
1981. The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. U.S. Fish Wildl. Serv., Biol. Serv. Program, FWS/OBS-81/15, 105 p.

Berg, J. A., and R. I. E. Newell.
1986. Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica*. Estuarine Coastal Shelf Sci. 23:375–386.

Butler, P. A.
1949. Gametogenesis in the oyster under conditions of depressed salinity. Biol. Bull. (Woods Hole) 96:263–269.

Chanley, P. E.
1958. Survival of some juvenile bivalves in water of low salinity. Proc. Natl. Shellfish. Assoc. 48:52–65.

Choi, K- S., D. H. Lewis, E. N. Powell, and S. M. Ray.
1993. Quantitative measurement of reproductive output in the American oyster, *Crassostrea virginica* (Gmelin), using an enzyme-linked immunosorbent assay (ELISA). Aquaculture Fish. Manag. 24:299–322.

Copeland, B.J., and H.D. Hoese.
1966. Growth and mortality of the American oyster, *Crassostrea virginica*, in high salinity shallow bays in central Texas. Publ. Inst. Mar. Sci. Univ. Tex. 11:149–158.

Crosby, M. P., C. F. Roberts, and P. D. Kenny.
1991. Effects of immersion time and tidal position on in situ growth rates of naturally settled eastern oysters, *Crassostrea virginica* (Gmelin, 1791). J. Shellfish Res. 10:95–103.

Cummins, K. W., and J. C. Wuycheck.
1971. Caloric equivalents for investigations in ecological energetics. Int. Ver. Theor. Angew. Limnol. Verh. 18:1–158.

Cummins, H., E. N. Powell, R. J. Stanton Jr., and G. Staff.
1986. The size-frequency distribution in palaeoecology: the effects of taphonomic processes during formation of death assemblages in Texas bays. Palaeontology (Lond.). 29:495–518.

Dame, R. F.
1972. The ecological energies of growth, respiration and assimilation in the intertidal American oyster *Crassostrea virginica*. Mar. Biol. (Berl.) 17:243–250.

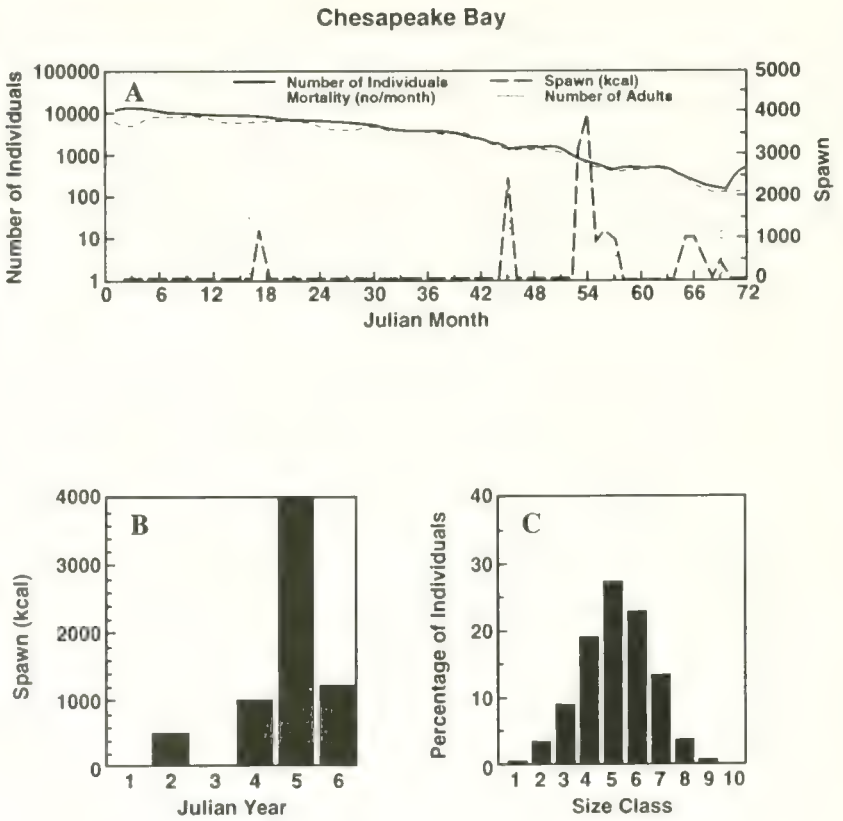

Figure 19
The time development of a simulated *Crassostrea virginica* population exposed to a seasonal temperature regime for Chesapeake Bay and summer mortality. Additional information in Figure 3 and Table 2, case 44.

Dekshenieks, M. M., E. E. Hofmann, and E. N. Powell.
In press. Environmental effects on the growth and development of *Crassostrea virginica* (Gmelin) larvae: a modeling study. J. Shellfish Res.

Deslous-Paoli, J- M., and M. Heral.
1988. Biochemical composition and energy value of *Crassostrea gigas* (Thunberg) cultured in the Bay of Marennes-Oleron. Aquat. Living Resour. 1:239–249.

Doering, P. H., and C. A. Oviatt.
1986. Application of filtration rate models to field populations of bivalves: an assessment using experimental mesocosms. Mar. Ecol. Prog. Ser. 31:265–275.

Dupuy, J. L., N. T. Windson, and C. E. Sutton.
1977. Manual for design and operation of an oyster seed hatchery. Virginia Institute of Marine Science, Gloucester Point, VA, 104 p.

Engle, J. B.
1947. Commercial aspects of the upper Chesapeake Bay oyster bars in light of the recent oyster mortalities. Proc. Natl. Shellfish. Assoc. for 1946, p. 42–46.

1956. Ten years of study on oyster setting in a seed area in upper Chesapeake Bay. Proc. Natl. Shellfish. Assoc. 46:88–99.

Engle, J. B., and A. Rosenfield.

1962. Progress in oyster mortality studies. Proc. Gulf Carib. Fish. Inst. 15:116–124.

Epifanio, C. E., and J. Ewart.

1977. Maximum ration of four algal diets for the oyster *Crassostrea virginica* Gmelin. Aquaculture 11: 13–29.

Fréchette, M., D. A. Booth, B. Myrand, and H. Bérard.

1991. Variability and transport of organic seston near a mussel aquaculture site. ICES Mar. Sci. Symp. 192:24–32.

Gallager, S. M., and R. Mann.

1986. Growth and survival of *Mercenaria mercenaria* (L.) and *Crassostrea virginica* (Gmelin) relative to broodstock conditioning and lipid content of eggs. Aquaculture 56:105–121.

Galtsoff, P. S.

1964. The American oyster *Crassostrea virginica* Gmelin. U.S. Fish Wildl. Serv. Fish. Bull. 64:1–480.

Galtsoff, P. S., W. A. Chipman Jr., J. B. Engle, and H. N. Calderwood.

1947. Ecological and physiological studies of the effect of sulphate pulp mill wastes on oysters in the York River, Virginia. U.S. Fish Wildl. Serv. Fish. Bull. 51:58–186.

Garton, D., and W. B. Stickle.

1980. Effects of salinity and temperature on the predation rate of *Thais haemastoma* on *Crassostrea virginica* spat. Biol. Bull. (Woods Hole) 158:49–57.

Gilmore, G. H., S. M. Ray, and D. V. Aldrich.

1975. Growth and mortality of two groups of oysters (*Crassostrea virginica* Gmelin), maintained in cooling water at an estuarine electric power generating station. Texas A&M Univ. Proj. Rep. TAMU-SG-75–207, 67 p.

Glude, J. B.

1966. Criteria of success and failure in the management of shellfisheries. Trans. Am. Fish. Soc. 95:260–263.

Gunter, G.

1955. Mortality of oysters and abundance of certain associates as related to salinity. Ecology 36:601–605.

Hayes, P. F., and R. W. Menzel.

1981. The reproductive cycle of early setting *Crassostrea virginica* (Gmelin) in the northern Gulf of Mexico, and its implications for population recruitment. Biol. Bull. (Woods Hole) 160:80–88.

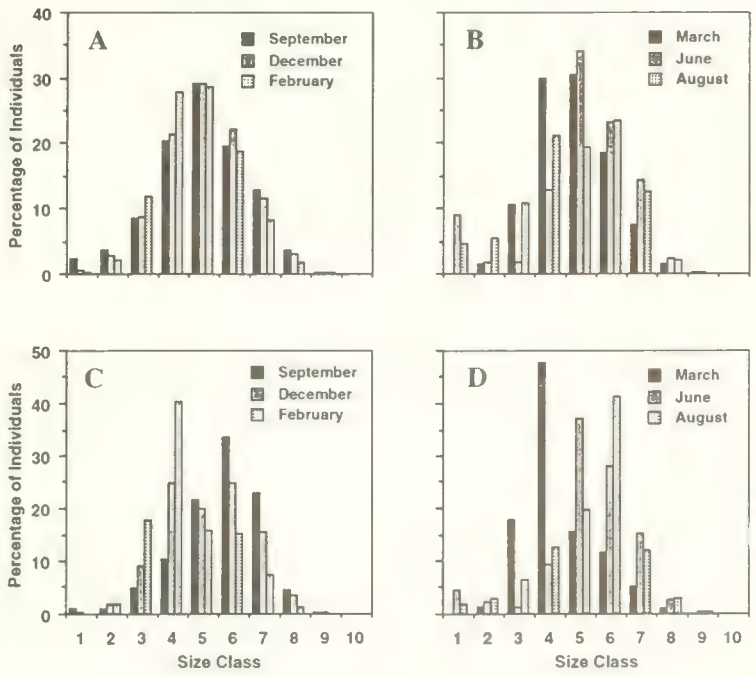

Figure 20

The seasonal shift in size-frequency distribution for two *Crassostrea virginica* populations in Chesapeake Bay. (**A** and **B**) exposed to summer mortality; (**C** and **D**) exposed to winter mortality. (A and B) coincide with the simulation depicted in Figure 19. (C and D) coincide with Table 2, case 51.

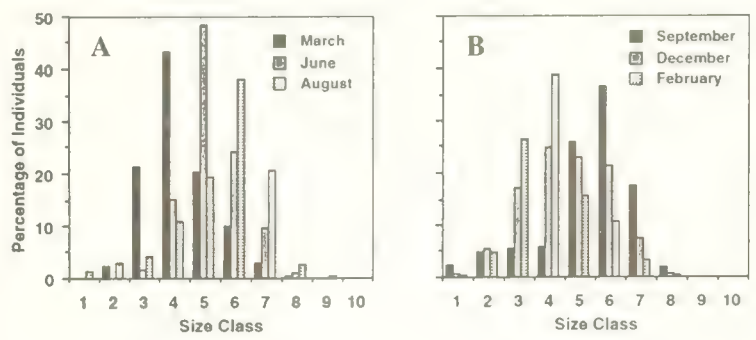

Figure 21

The seasonal shift in size-frequency distribution of a *Crassostrea virginica* population in Chesapeake Bay exposed to an (**A**) early spring (March/April) and (**B**) early fall (August/September) bloom. The complementary case of two later blooms is depicted in Figure 20, C and D. More information can be found in Table 2, case 48.

Hofmann, E. E., E. N. Powell, J. M. Klinck, and E. A. Wilson.
1992. Modeling oyster populations. III: Critical feeding periods, growth and reproduction. J. Shellfish Res. 11:399–416.

Hofmann, E. E., J. M. Klinck, E. N. Powell, S. Boyles, and M. Ellis.
In press. Modeling oyster populations. II: Adult size and reproductive effort. J. Shellfish Res.

Hofstetter, R. P.
1966. Oyster mortality studies along the Texas coast during 1966. Texas Parks Wildl. Dept. Coastal Fish. Proj. Rep., p. 55–68.
1983. Oyster population trends in Galveston Bay 1973–1978. Tex. Parks Wildl. Dept. Management Data Ser. no. 51, 33 p.

Hofstetter, R. P., and S. M. Ray.
1988. Managing public oyster reefs: Texas experience. J. Shellfish Res. 7:213.

Hofstetter, R. P., T. L. Heffernan, and B. D. King III.
1965. Oyster (*Crassostrea virginica*) mortality studies along the Texas coast. Tex. Parks Wildl. Dep. Coastal Fish. Proj. Rep., p. 119–131.

Kennedy, V. S.
1982. Sex ratios in oysters, emphasizing *Crassostrea virginica* from Chesapeake Bay, Maryland. Veliger 25:329–338.

Klinck, J. M., E. N. Powell, E. E. Hofmann, E. A. Wilson, and S. M. Ray.
1992. Modeling oyster populations: the effect of density and food supply on production. Proc. Adv. Mar. Technol. Conf. 5:85–195.

Koehn, R. K., and B. L. Bayne.
1989. Towards a physiological and genetical understanding of the energetics of the stress response. Biol. J. Linn. Soc. 37:157–171.

Laird, M.
1961. Microecological factors in oyster epizootics. Can. J. Zool. 39:449–485.

Lee, R. F., and P. B. Heffernan.
1991. Lipids and proteins in eggs of eastern oysters (*Crassostrea virginica* Gmelin, 1791) and northern quahogs (*Mercenaria mercenaria* Linnaeus, 1758). J. Shellfish Res. 10:203–206.

Loosanoff, V. L.
1958. Some aspects of behavior of oysters of different temperatures. Biol. Bull. (Woods Hole) 114:57–70.

Loosanoff, V. L., and F. D. Tommers.
1948. Effect of suspended silt and other substances on rate of feeding of oysters. Science (Wash. D.C.) 107:69–70.

Lund, E. J.
1957. A quantitative study of clearance of a turbid medium and feeding by the oyster. Publ. Inst. Mar. Sci. Univ. Tex. 4:296–312.

MacKenzie, C. L., Jr.
1989. A guide for enhancing estuarine molluscan shellfisheries. Mar. Fish. Rev. 51(3):1–47.

Mackin, J. G.
1959. A method of estimation of mortality rates in oysters. Proc. Natl. Shellfish. Assoc. 50:41–51.

Mackin, J. G., and S. H. Hopkins.
1962. Studies on oyster mortality in relation to natural environments and to oil fields in Louisiana. Publ. Inst. Mar. Sci. Univ. Tex. 7:1–131.

Mackin, J. G., and A. K. Sparks.
1962. A study of the effect on oysters of crude oil loss from a wild well. Publ. Inst. Mar. Sci. Univ. Tex. 7:230–261.

Mackin, J. G., and D. A. Wray.
1950. Report on the second study of mortality of oysters in Barataria Bay, Louisiana, and adjacent areas. Texas A&M Research Foundation Proj. Rep., Proj. 9, 39 p.

Mackin, J. G., B. Welch, and C. Kent.
1950. A study of mortality of oysters of the Buras area of Louisiana. Texas A&M Research Foundation Proj. Rep., Proj. 9, 41 p.

Menzel, R. W.
1950a. Report on oyster studies in Caillou Island oil field, Terrebonne Parish Louisiana. Texas A&M Research Foundation Proj. Rep., Proj. 9, 60 p.
1950b. Report of oyster studies in Lake Felicity and Bayou Bas Bleu, Terrebonne Parish, Louisiana. Texas A&M Research Foundation Proj. Rep., Proj. 9, 46 p.

Menzel, R. W., and S. H. Hopkins.
1953. Report on oyster experiments at Bay Sainte Elaine oil field. Texas A&M Research Foundation Proj. Rep., Proj. 9, 170 p.

Menzel, R. W., N. C. Hulings, and R. R. Hathaway.
1957. Causes of depletion of oysters in St. Vincent Bar, Apalachicola Bay, Florida. Proc. Natl. Shellfish. Assoc. 48:66–71.

Moore, H. F., and T. E. B. Pope.
1910. Oyster culture experiments and investigations in Louisiana. U.S. Dep. Commerce Labor Bur. Fish. Document No. 731, 52 p.

Mountford, K., and R. C. Reynolds.
1988. Potential biological effects of modeled water quality improvements resulting from two pollutant reduction scenarios. *In* Understanding the estuary: advances in Chesapeake Bay research. Proceedings of a conference 29–31 March 1988. Chesapeake Research Consortium Publ. 129, Baltimore, MD, p. 593–606.

Needler, A. W. H., and R. R. Logie.
1947. Serious mortalities in Prince Edward Island oysters caused by a contagious disease. Trans. R. Soc. Canada Ser. III Sect. V 41:73–89.

Newell, R. I. E.
1985. Physiological effects of the MSX parasite *Haplosporidium nelsoni* (Haskin, Stauber & Mackin) on the American oyster *Crassostrea virginica*. J. Shellfish Res. 5:91–95.

Osman, R. W., R. B. Whitlatch, and R. N. Zajac.
1989. Effects of resident species on recruitment into a community: larval settlement versus post-

settlement mortality in the oyster *Crassotrea virginica*. Mar. Ecol. Prog. Ser. 54:61–73.

Owen, H. M.
1953. Growth and mortality of oysters in Louisiana. Bull. Mar. Sci. Gulf Caribb. 3:44–54.

Powell, E. N., H. Cummins, R. J. Stanton Jr., and G. Staff.
1984. Estimation of the size of molluscan larval settlement using the death assemblage. Estuarine Coastal Shelf Sci. 18:367–384.

Powell, E.N., M.E. White, E.A. Wilson, and S.M. Ray.
1987. Small-scale spatial distribution of oysters (*Crassostrea virginica*) on oyster reefs. Bull. Mar. Sci. 41:835–855.

Powell, E. N., E. E. Hofmann, J. M. Klinck, and S. M. Ray.
1992. Modeling oyster populations.I: A commentary on filtration rate. Is faster always better? J. Shellfish Res. 11:387–398.

Prytherch, H. F.
1929. Investigation of the physical conditions controlling spawning of oysters and the occurrence, distribution, and setting of oyster larvae in Milford Harbor, Connecticut. Bull. Bur. Fish. 44:429–503.

Quast, W. D., M. A. Johns, D. E. Pitts Jr., G. C. Matlock, and J. E. Clark.
1988. Texas oyster fishery management plan source document. Texas Parks Wildl. Dept Coastal Fish. Branch, Austin, TX, 178 p.

Ray, S. M., and A. C. Chandler.
1955. *Dermocystidium marinum*, a parasite of oysters. Exp. Parasitol. 4:172–200.

Schlesselman, G. W.
1955. The Gulf coast oyster industry in the U.S. Geogr. Rev. 45:531–541.

Shumway, S. E., and R. K. Koehn.
1982. Oxygen consumption in the American oyster *Crassostrea virginica*. Mar. Ecol. Prog. Ser. 9:59–68.

Sindermann, C. J.
1968. Oyster mortalities, with particular reference to Chesapeake Bay and the Atlantic coast of North America. U.S. Fish Wildl. Serv. Bur. Comm. Fish. Spec. Sci. Rep. Fisheries No. 569, 10 p.

Soniat, T. M., and S. M. Ray.
1985. Relationships between possible available food and the composition, condition and reproductive state of oysters from Galveston Bay, Texas. Contrib. Mar. Sci. 28:109–121.

Soniat, T. M., and M. S. Brody.
1988. Field validation of a habitat suitability index model for the American oyster. Estuaries 11:87–95.

Soniat, T. M., S. M. Ray, and L. M. Jeffrey.
1984. Components of the seston and possible available food for oysters in Galveston Bay, Texas. Contrib. Mar. Sci. 27:127–141.

Soniat, T. M., L. E. Smith, and M. S. Brody.
1989. Mortality and condition of the American oyster in Galveston Bay, Texas. Contrib. Mar. Sci. 31:77–94.

Stanley, J. G., and M. A. Sellers.
1986. Species profile: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico)—American oyster. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.64), U.S. Army Corps of Engineers, TR EL-82–4, 25 p.

Stickle, W. B.
1985. Effects of environmental factor gradients on scope for growth in several species of carnivorous marine invertebrates. *In* J. S. Gray and M. E. Christiansen (eds.), Marine biology of polar regions and effects of stress on marine organisms. John Wiley & Sons Ltd., New York, p.601–616.

Underwood, A. J.
1989. The analysis of stress in natural populations. Biol. J. Linn. Soc. 37:51–78.

White, M. E., E. N. Powell, and S. M. Ray.
1988. Effects of parasitism by the pyramidellid gastropod *Boonea impressa* on the net productivity of oysters (*Crassostrea virginica*). Estuarine Coastal Shelf Sci. 26:359–377.

Wright, D. A., and E. W. Hetzel.
1985. Use of RNA:DNA ratios as an indicator of nutritional stress in the American oyster *Crassostrea virginica*. Mar. Ecol. Prog. Ser. 25:199–206.

Young, P. C., and R. B. Martin.
1989. The scallop fisheries of Australia and their management. Crit. Rev. Aquat. Sci. 1:615–638.

Zonneveld, C.
1991. Estimating death rates from transect counts. Ecol. Entomol. 16:115–121.

A suite of extensions to a nonequilibrium surplus-production model*

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Abstract.—Surplus-production models, because of their simplicity and relatively undemanding data needs, are attractive tools for many stock assessments. This paper reviews the logistic production model, starting with the basic differential equation and continuing with a description of the model development without the equilibrium assumption. It then describes several extensions, including "tuning" the model to a biomass index; partitioning fishing mortality by gear, time, or area; and making projections. Computation of confidence intervals on quantities of interest (e.g. maximum sustainable yield (MSY), effort at MSY, level of stock biomass relative to the optimum level) can be done through bootstrapping, and the bootstrap can also be used to construct nonparametric tests of hypotheses about changes in catchability. To fit the model, an algorithm that uses a forward solution of the population equations can be implemented on a small computer. An example of the utility of surplus-production models (illustrating several of these extensions) is given. The example is loosely based on swordfish (*Xiphias gladius*) in the North Atlantic Ocean, but is not intended to describe the actual status of that stock.

Despite the prevalence of age-structured population models, surplus-production models—which generally do not incorporate age structure—remain useful for analysis of fish population dynamics. These models are of particular value when the catch cannot be aged, or cannot be aged precisely, and therefore age-structured models cannot be applied. Surplus-production models are also useful as a complement to age-structured models, providing another view of the data and the fisheries. An especially appealing aspect of production models is their simplicity; from a scientific point of view, this makes exploration of their properties easier; from a management point of view, it makes their results easier to present and understand (Barber, 1988).

In this paper, I show that another benefit of these models' simplicity is that model extensions are easily made. Examples of such extensions include modeling several simultaneous or sequential fisheries on the same stock, "tuning" the model to a biomass index (as is often done in age-structured models; e.g. the CAGEAN model of Deriso et al., 1985; the CAL model of Parrack, 1986; the ADAPT model of Gavaris, 1988), modeling changes in catchability or population characteristics (e.g. carrying capacity), and estimating missing values of fishing effort. Many of these extensions have not been presented before.

The comprehensiveness of a production model can be further increased by introducing another extension: computation of nonparametric estimates of variability in the results. These can be obtained by bootstrapping, and can be used both to describe the results more completely and to learn more about the model's behavior under a variety of circumstances.

After reviewing the formulation of the simplest surplus-production model (the logistic model), a number of extensions to the model are described. An example, loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean, is presented to illustrate typical results from the model and the use of many of the extensions. The example, which is not intended to be an assessment of that stock, should not be used to make inferences about stock status.

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Model formulation and fitting

Basic differential equations

Surplus-production models characterize a population as an undifferentiated biomass. The number of individuals present or harvested plays no part in these models, nor is age or size structure considered. A quantity termed "surplus production" is used to characterize population dynamics at different levels of population size (measured in biomass). Surplus production is the algebraic sum of three major forces: recruitment, growth, and natural mortality. The adjective "surplus" refers to the surplus of recruitment and growth over natural mortality; i.e. the net production. In this article, surplus production will often be termed simply "production," and the models termed "production models."

In the simplest production model, the logistic or Graham-Schaefer (Graham, 1935; Schaefer, 1954, 1957) model, a first–order differential equation describes the rate of change of stock biomass B_t due to production. In the absence of fishing, the population's rate of increase or decrease is assumed to be a function of the current population size only:

$$\frac{dB_t}{dt} = rB_t - \frac{r}{K}B_t^2, \tag{1}$$

where B_t is the population biomass at time t and r and K are parameters. The right side of Equation 1 is simply the start of the Taylor expansion of an arbitrary function $\Phi(B)$ passing through the origin (Lotka, 1924).

Equation 1 is written in the parameterization of population ecology, in which K represents the maximum population size, or carrying capacity, and r represents the stock's intrinsic rate of increase (in proportion per unit time). In this paper, both are assumed constant. Other parameterizations could be used, and indeed a slightly different parameterization is used for simplicity in the next section.

Adding fishing mortality F_t to the model, it becomes

$$\frac{dB_t}{dt} = (r - F_t)B_t - \frac{r}{K}B_t^2. \tag{2}$$

This model, like many fisheries models, is much simpler than the real world. In particular, it excludes such factors as environmental variation, interspecific effects, or the possible presence of more than one stable regime.

Time trajectories of biomass and yield

Integration of Equation 2 with respect to time allows modeling the biomass and yield through time. Before integration, simplify notation by defining $\alpha_t = r - F_t$ and $\beta = r/K$ to express Equation 2 more simply as

$$\frac{dB_t}{dt} = \alpha_t B_t - \beta B_t^2. \tag{3}$$

Equation 3 can be conveniently solved for biomass under the assumption that F_t is constant and that therefore α_t is constant. This is a weak assumption, for if F_t varies, time can be divided into short periods of constant or nearly constant F and a solution found for each period. Fitting would then require knowing the catch and effort for each short period.

For the period beginning at $t = h$ and ending at time $t = h + \delta$, during which the instantaneous fishing mortality rate is F_h, the solution to Equation 3 is

$$B_{h+\delta} = \frac{\alpha_h B_h e^{\alpha_h \delta}}{\alpha_h + \beta B_h (e^{\alpha_h \delta} - 1)} \quad \text{when } \alpha_h \neq 0, \text{ or} \tag{4a}$$

$$B_{h+\delta} = \frac{B_h}{1 + \beta \delta B_h} \quad \text{when } \alpha_h = 0. \tag{4b}$$

Equation 4a is the familiar logistic equation. However, if $\alpha_h = 0$ (i.e. if $F_h = r$), Equation 4a is undefined and Equation 4b is used in its place.

Modeling the yield during the same period involves another integration with respect to time:

$$Y_h = \int_{t-h}^{h+\delta} F_h B_t \, dt, \tag{5}$$

where B_t, the biomass at instant t, is defined by Equations 4a and 4b; F_h is the (constant) instantaneous rate of fishing mortality during the time period; and Y_h is the yield taken during the period. Performing the integration in Equation 5,

$$Y_h = \frac{F_h}{\beta} \ln\left[1 - \frac{\beta B_h (1 - e^{\alpha_h \delta})}{\alpha_h}\right] \quad \text{when } \alpha_h \neq 0, \text{ or} \tag{6a}$$

$$Y_h = \frac{F_h}{\beta} \ln(1 + \delta \beta B_h) \quad \text{when } \alpha_h = 0. \tag{6b}$$

Equation 6a was apparently first given by Pella (1967) (and a similar form developed by Schnute [1977]); Equations 4b and 6b seem not to have been presented in fishery biology before now.

It follows from the definition of F that the estimated average biomass during the period is simply Y_h / F_h. The surplus production P_h during the time period can be determined by mass balance:

$$P_h = B_{h+\delta} - B_h + Y_h. \tag{7}$$

When yield is equal to surplus production, the population is in equilibrium.

Parameter estimation

Parameter estimation for this model can be accomplished by a number of methods. The method presented here is a slight modification of one originated by Pella (1967), later used by Pella and Tomlinson (1969), and recently termed the "time-series method" by Hilborn and Walters (1992). Although it is not necessary to use equal time periods, the treatment in the balance of this paper assumes, for simplicity, that there are T equal time periods, indexed by $\tau = \{1, 2, ..., T\}$, and that a period is one year in duration. The following symbols are used:

B_τ population biomass at the start of year τ
Y_τ yield in biomass during year τ
P_τ surplus production during year τ,
f_τ fishing effort rate during year τ,
F_τ fishing mortality rate during year τ,
α_τ function of F_τ; $\alpha_\tau = r - F_\tau$.

Estimates of the first five of these quantities are represented by $\hat{B}_\tau, \hat{Y}_\tau, \hat{P}_\tau, \hat{f}_\tau$, and $\hat{F}_\tau$.

An important additional assumption is that, for all τ, $F_\tau = qf_\tau$; in other words, that fishing mortality rate is proportional to fishing effort rate and that the catchability coefficient q is constant. (The assumption of constant q is slightly relaxed later.)

The data required for fitting are, for each time period τ, data on effort f_τ and the yield Y_τ, where $\tau = \{1, 2, ..., T\}$ and $T > 4$. The parameters to be estimated are r and K in Equation 1, q, and B_1, the biomass at the beginning of the first year. The simplest procedure accumulates residuals in yield. To perform the estimation, the following algorithm is used:

A1 Obtain starting guesses for the four parameters.
A2 Beginning with the current estimate of B_1, project the population through time according to Equations 4a and 4b. For each year of the projection, compute estimated yield from Equations 6a and 6b.
A3 Compute the objective function to be minimized. Assuming a multiplicative error structure in yield, this is

$$\sum_{\tau=1}^{T}\left[\log(Y_\tau) - \log(\hat{Y}_\tau)\right]^2.$$

A4 Monitor the objective function for convergence. If achieved, end. Otherwise, revise the parameter estimates (using a standard minimization scheme) and continue at step A2.

The simplex or "polytope" algorithm (Nelder and Mead, 1965; Press et al., 1986) works well as the minimization scheme in this application. Although not as rapid computationally as some other methods, the simplex algorithm is quite robust to starting values and is easily manipulated (by restarts) to avoid local minima (see Press et al., 1986, p. 292). Rivard and Bledsoe (1978) used the Marquardt (1963) algorithm successfully for estimation in a similar model.

The estimation method just described uses the recorded effort in each year to estimate yield. Alternatively, one could use the recorded yield in each year to estimate the fishing mortality rate (or equivalently, the fishing effort rate). The solutions of Equations 6a and 6b for fishing mortality rate are

$$F_\tau = \frac{\beta Y_\tau}{\ln\left[\dfrac{\beta B_t\left(e^{\alpha_\tau} - 1\right)}{\alpha_\tau} + 1\right]} \quad \text{when } \alpha_\tau \neq 0, \text{ or} \tag{8a}$$

$$F_\tau = \frac{\beta Y_\tau}{\ln\left[1 + \beta B_\tau\right]} \quad \text{when } \alpha_\tau = 0. \tag{8b}$$

To use this approach, one must revise the second and third steps of the algorithm to become—

A2′ Beginning with the current estimate of B_1, compute the estimated fishing effort for each year by solving Equation 8a or 8b and dividing by $\hat{q}$. Project the population to year-end with Equation 4.
A3′ Compute the objective function to be minimized. Assuming a multiplicative error structure in effort, this is

$$\sum_{\tau=1}^{T}\left[\log(f_\tau) - \log(\hat{f}_\tau)\right]^2.$$

This is equivalent to minimizing the sums of squared residuals in the logarithm of catch per unit of effort, i.e. to minimizing

$$\sum_{\tau=1}^{T}\left[\log(C_\tau / f_\tau) - \log(C_\tau / \hat{f}_\tau)\right]^2.$$

A significant practical advantage of the second approach is that it simplifies the analysis of data with some missing data on effort. During parameter estimation, effort is estimated for all years; for years of missing effort, the contribution to the objective function is simply defined to be zero. In contrast, the computations for the first approach are not possible without data on effort for each year.

Estimating effort from yield introduces two small practical difficulties. The first difficulty is that Equation 8a is not an explicit solution for effort (because α_τ includes f_τ), so it must be solved iteratively. This is accomplished by putting a starting guess $\tilde{F}_\tau$ into the right–hand side of the equation, solving, and substituting the result repeatedly until convergence is achieved. A logical starting guess is $\tilde{F}_\tau = Y_\tau / \hat{B}_\tau$.

The second difficulty involves a fundamental difference between predicting yield and predicting effort. For a given starting biomass and effort, one can always compute the corresponding yield. For a given starting biomass, however, there are some yields that can never be obtained, no matter how high the effort. Under these circumstances, the catch equation (6a or 6b) has no solution. Unless a tactic is devised for such cases, it becomes impossible to compute the objective function when they occur, and thus impossible to conduct its minimization. A tactic suggested by R. Methot[1] as useful in his stock-synthesis model (Methot, 1989, 1990) is to place a constraint on the maximum allowable value of F_τ (and consequently of f_τ). When an estimate of F_τ reaches this constraint, it is not allowed to increase further, and the quantity $[\log(Y_\tau) - \log(\hat{Y}_\tau)]^2$ is added to the objective function along with the usual squared residual in effort. This allows computation of a reasonable value of the objective function for such regions of the solution space that may be encountered during optimization. In my experience, however, final estimates have always come from a solution in which yield is always matched exactly.

In fitting a linear regression, observation error in the predictor variables causes problems with the parameter estimates, including inconsistency and, in the bivariate linear case, bias towards zero (Thiel, 1971; Kennedy,1979). The problems induced into nonlinear models are less well understood, but are believed to be similar. Schnute (1989) has illustrated how the choice of dependent variable in a fisheries model can affect the results substantially. In fisheries contexts, yield is usually observed more precisely than fishing effort; for that reason, it seems preferable on statistical grounds to use the second approach, estimating effort from yield, rather than estimating yield from effort.

Whichever approach is chosen, the estimation process results in direct estimates of B_1, r, K, and q, which define unique estimates of the stock biomass levels B_2, B_3, ..., B_T and the stock's production during each period of time. The corresponding estimate of maximum sustainable yield (MSY) under the logistic model is $\widehat{\mathrm{MSY}} = \hat{K}\hat{r}/4$. According to the theory of production modeling, MSY can be attained as a sustainable yield only at one specific stock size; for the logistic model this is $B_{\mathrm{MSY}} = K/2$, estimated by $\hat{B}_{\mathrm{MSY}} = \hat{K}/2$. The instantaneous fishing mortality that generates MSY at B_{MSY} is $F_{\mathrm{MSY}} = r/2$; the corresponding rate of fishing effort is $f_{\mathrm{MSY}} = r/2q$, with estimates given by substituting $\hat{r}$ and $\hat{q}$ for the unknown true values in these two expressions.

[1] Methot, R. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun., 1993.

The logarithmic objective function assumes multiplicative errors with constant variance. The solution obtained is the maximum-likelihood solution if the transformed residuals are independent, of constant variance, and normally distributed (see Seber and Wild, 1989). However, maximum-likelihood methods, while generally desirable, are not necessarily robust to outliers, nor do they necessarily have desirable small-sample properties. Use of a robust-regression method (such as least absolute values regression) would be an interesting research topic.

Another management benchmark

An analogue of the management benchmark $F_{0.1}$ can be computed for this model (or for any production model). The derivative of equilibrium yield with respect to fishing mortality rate for this model is

$$\frac{dY_e}{dF} = K\left(1 - \frac{2F}{r}\right). \tag{9}$$

At $F = 0$, this derivative is equal to K. We define as $F_{0.1}$ for this model as the value of F at which Equation 9 equals $0.1K$. Substitution into Equation 9 gives the following results: $F_{0.1} = 0.45r$, and $Y_{0.1} = 0.2475rK$ (where $Y_{0.1}$ is the equilibrium yield corresponding to $F_{0.1}$). An equivalent statement is that $F_{0.1}$ is 90% of F_{MSY}, and $Y_{0.1}$ is 99% of MSY. Punt (1990) used the concept of $F_{0.1}$ for a production model but did not explicitly state these relationships.

Penalty for large estimates of B_1

Logistic production theory implies that B_1 should always be less than K, but the objective functions used here are relatively insensitive to the estimate of B_1. In practice, I have found that the estimate of B_1 obtained from some data sets tends to be much larger than the estimate of K. Such results could be eliminated by introducing a fixed constraint into the solution, but I have used another method successfully: adding a penalty term to the objective function when $\hat{B}_1 > \hat{K}$. Including this term, the complete logarithmic objective function (assuming residuals in effort) becomes

$$L = \sum_{\tau=1}^{T}\left[\log(f_\tau) - \log(\hat{f}_\tau)\right]^2 + \phi\left[\log(\hat{B}_1) - \log(\hat{K})\right]^2, \tag{10}$$

where $\phi \equiv 1$ if $\hat{B}_1 > \hat{K}$, and $\phi \equiv 0$, otherwise. While constraining the value of B_1 seems logical in accordance with the underlying population theory, such constraints can change the estimates of other parameters, compared to an unconstrained solution. The amount of change can be examined by estimating with and without the penalty term or fixed constraint.

Extensions to the model

A great strength of the model presented here is the ease with which it can be extended and modified. Such extensions can include, for example, modeling fisheries divided by space, time, or gear type; analyzing data series including some years of no effort, as would occur during a closure; analyzing data series with years of missing or highly uncertain effort data; incorporating changes in catchability within the data series, perhaps after periods of closure or following regulatory changes; and tuning the model to fishery-independent estimates or indices of population biomass.

Missing data

Gaps in the effort and yield time series do not present a problem to these dynamic production model analyses. Years with no effort (and therefore no catch) can easily be treated by defining the residual to be zero. Although such years do not influence parameter estimation directly, the time lag during the years of closure carries information that is incorporated in fitting the model, and an estimate of population biomass for each missing year is made according to the logistic growth model. In contrast, years of closure contribute no information to production models that assume equilibrium conditions.

A slightly more difficult problem is the correct treatment of years in which effort is known to have existed, but for which the data are missing or highly uncertain. In such a case, the framework presented here can be used to estimate, simultaneously with the other parameters, effort levels for a limited number of such years within the series. As in any estimation scheme, the total number of estimated parameters should be kept reasonably small in comparison to the number of years of nonzero data. If residuals are constructed in effort (rather than yield) the estimation of missing effort becomes trivial, as a predicted effort is computed for each year during parameter estimation.

More than one data series

Another simple extension of the basic estimation framework is analysis of stocks fished by two or more different gear types, either in the same years or serially. For convenience, I refer to these as different fisheries on the same stock. To define the situation more precisely, there are J different fisheries, indexed by $j = \{1, 2, ..., J\}$. The effort applied by fishery j in period τ is $f_{i\tau}$, the catchability coefficient of that fishery is q_j, and the yield in period τ is $Y_{i\tau}$. All q_j are assumed time–invariant. The total instantaneous fishing mortality in period τ is

$$F_\tau = \sum_{j=1}^{J} q_j f_{j\tau}. \tag{11}$$

Biomass and yield projections can be computed by Equations 4a, 4b, 6a, and 6b as before. The estimated yield from fishery j in period τ is

$$\hat{Y}_{j\tau} = \frac{\hat{q}_j \hat{f}_{j\tau}}{\hat{F}_\tau} \hat{Y}_\tau, \tag{12}$$

where $\hat{Y}_\tau$ is the total yield in period τ. During parameter estimation, a residual is obtained for each fishery having nonzero effort in period τ. The contribution to the objective function for each period is thus composed of a sum of terms, one for each fishery with nonzero effort. In addition, the individual fisheries may carry different statistical weights to reflect varying levels of confidence in the data from each fishery. Inverse-variance weighting can be approximated by iteratively examining the mean-squared error (MSE) from each series, weighting, and re-estimating the parameters.

Model tuning

If an external series of population biomass estimates is available, it can be incorporated into the analysis in a procedure analogous to tuning an age-structured analysis. The external estimates are compared to the population estimates derived within the production model and the residuals incorporated in computation of the objective function. Rivard and Bledsoe (1978) suggested this possibility, but did not pursue the idea, and it has also been described by Hilborn and Walters (1992). The external biomass series need not be continuous, but may contain missing values; the series' contribution to the objective function is set to zero for years with missing values. An external *index* of biomass can be used similarly, with the cost of estimating one more parameter (the catchability associated with the index).

The model formulation involved in tuning the model is similar to that used when fitting more than one fishery. As in that situation, each year's contribution to the objective function consists of a sum of terms. Here, the sum includes a term from each fishery and a term for each biomass–estimate or index series. For a maximum–likelihood solution, the components should carry statistical weights inversely proportional to their variances.

Varying catchability

In many situations, catchability is thought to change relatively suddenly, perhaps because more efficient

gear for finding or catching the fish is introduced. In such cases, the formulation represented by Equations 11 and 12 can be used to estimate different catchability coefficients for segments of a single time series. In formulating such a model, the time segments would be treated as separate fisheries, each having nonzero catch and effort data only during its respective time period. Each additional time segment would add one additional parameter to the model.

A common concern is determining whether the improvement in fit obtained from a more complex model is statistically significant. A production model with added catchability parameters can be tested against the simpler model (with one estimated q) with a standard F-ratio test. (Here F refers to the F distribution of statistics, not to fishing mortality rate.) The test statistic F^* is

$$F^* = \frac{(SSE_s - SSE_c)/v_1}{SSE_c/v_2}, \qquad (13)$$

where SSE_s and SSE_c are the error sums of squares of the simple and complex models, respectively; v_1 is the difference in number of estimated parameters between the two models; and v_2 is the number of data points less the total number of estimated parameters. The significance probability of F^* can be obtained from tables of the F-distribution with v_1 and v_2 degrees of freedom. As pointed out by a referee, this is equivalent to to a likelihood-ratio test assuming log-normal error structure, which is implicit in using the SSE from log-transformed data. Because of the possibility of specification error, any such significance test must be considered approximate.

A nonparametric test of the null hypothesis $q_1 = q_2$ can also be conducted by examining a bias-corrected confidence interval on the ratio of the two catchability coefficients. (Construction of bias-corrected confidence intervals is described later.) As an example, assume that the alternative hypothesis is $q_1 \neq q_2$. The null hypothesis would be rejected at $P<0.05$ if a 95% confidence interval on the ratio q_1 / q_2 did not include the value 1.0. Like the F-test, this test is approximate because of the possibility of specification error.

In other cases, catchability is thought to vary in more subtle ways than the step function just suggested (Paloheimo and Dickie, 1964; Gulland, 1975; MacCall, 1976; Peterman and Steer, 1981; Winters and Wheeler, 1985), and one could incorporate any number of catchability models into the estimation framework. It would be straightforward to model a linear trend (increase or decrease) in catchability with time. This could be parameterized by estimating the first and last years' values of q and generating intermediate years' values by linear interpolation, so that only one additional parameter would be estimated. One could also add some form of density–dependent catchability model with a minimal cost in terms of number of parameters estimated; the foundation of such an approach was presented by Fox (1975). However, it might prove difficult to distinguish varying catchability from trends in biomass itself. If so, the use of external estimates or indices of biomass, as explained above, might be especially valuable.

Bootstrap estimates of bias and variability

The bootstrap (Efron, 1982; Stine, 1990) is a sample reuse technique often used to estimate sampling variances, confidence intervals, bias, and similar properties of statistics, including parameter estimates. Major advantages of the bootstrap, compared to alternative methods (such as those based on the information matrix), are its flexibility and relative freedom from distributional assumptions. A minor drawback is that it demands a great deal of computer time.

Bootstrapping is often performed by resampling the original observations. However, in fitting nonequilibrium production models, the order of the catch-effort pairs is as significant as the data themselves. For time-series models (in the broad sense), Efron and Tibshirani (1986) describe a method, used here, that preserves the original time structure of the data. For each bootstrap trial (of which there may be 250 to several thousand), a set of synthetic observations is constructed by combining the ordered predictions from the original fit with residuals chosen at random (with replacement) from the set of residuals from the original fit. The model is then refit to this set of synthetic observations.

The bootstrap can be used to estimate bias in parameter estimates. The median estimation bias B_θ in a parameter θ is estimated by

$$\hat{B}_\theta = \hat{\theta}_m - \hat{\theta}, \qquad (13a)$$

where $\hat{\theta}$ is the conventional estimator of θ, and $\hat{\theta}_m$ is the median value of θ obtained from the bootstrap trials (Efron,1982; Efron and Gong, 1983). A bias–corrected estimator $\hat{\theta}_{BC}$ of a parameter θ can therefore be given by

$$\hat{\theta}_{BC} = \hat{\theta} - \hat{B}_\theta. \qquad (13b)$$

It appears that the median bias correction, rather than a mean correction, has been adopted in the bootstrapping literature because a mean correction (which would be expected to produce an "unbiased" estimate in the usual sense) can have extremely high variance (Hinkley, 1978). The resulting problems are

avoided by use of a median correction, which is quite resistent to outliers. However, the use of a median correction implies that the estimated bias correction will be nonzero for an estimator that is unbiased (in the usual sense) but arises from a distribution in which the median does not equal the mean. That is, the use of a median bias correction transforms the estimator into a median estimator.

Several methods have been developed for computing bias–corrected confidence intervals from the bootstrap (Efron, 1982; Efron, 1987; Noreen, 1989). The most widely used at present appears to be the BC method of Efron (1982). To compute a BC interval, let $N(z)$ be the cumulative distribution function (CDF) of the standard normal distribution and let N^{-1} be the inverse–normal CDF. Let $\hat{C}$ be the empirical bootstrap CDF of the parameter θ; i.e. $\hat{C}(g)$ is the proportion of realizations of $\hat{\theta}$ in the bootstrap distribution that falls below any arbitrary value g. Define the constant

$$z_0 = N^{-1}\left[\hat{C}(\hat{\theta})\right], \tag{14}$$

where $\hat{\theta}$ is the conventional estimator. Then, the $(1 - 2a)$ BC central confidence interval on $\hat{\theta}$ is defined as

$$\theta \in \left\{\hat{C}^{-1}\left[N\left(2z_0 + N^{-1}(a)\right)\right], \hat{C}^{-1}\left[N\left(2z_0 - N^{-1}(a)\right)\right]\right\}. \tag{15}$$

This method assumes that a transformation exists under which the distribution of θ becomes normal and homoscedastic. However, the form of the transformation need not be known (Efron and Gong, 1983). Kizner (1991) constructed bootstrap confidence intervals on production-model results, but he did not state whether bias corrections were used.

This discussion of bootstrapping has referred to estimated "parameters" for simplicity, but the method can be used to estimate bias corrections and bias–corrected confidence intervals for any estimated quantity. Such quantities might include estimates of MSY, f_{MSY}, the population biomass in the final (or any other) year, $f_{0.1}$, projections of biomass levels (discussed next), and so forth.

Projections

Because a production model implicitly includes a recruitment function, it can be used to make projections based on hypothetical catch or effort quotas. As noted above, the historical population biomass trajectory is estimated during parameter estimation. The modeled population can then be projected forward in time by using the same population equations (4, 6, 8), and a proposed set of yields or effort rates. If the bootstrap is used following parameter estimation, the results of each bootstrap trial can be projected forward. From the results, it is possible to compute bias–corrected point estimates and confidence intervals on the projection results.

Example: North Atlantic swordfish

Many aspects of the production model discussed above are illustrated in this example, which is loosely based on swordfish, *Xiphias gladius,* in the North Atlantic Ocean. The example comprises two analyses, the difference between them being the use of an abundance index for tuning the second analysis. Both the base analysis and the tuned analysis used the same yield and fishing-effort data (Table 1; Fig. 1); the tuned analysis also used a hypothetical index of abundance constructed for this purpose (Table 1; Fig. 1). In both analyses, errors were assumed to occur in fishing effort and to follow a lognormal distribution; in other words, the "second estimation approach" described previously was used. Each analysis included a projection of five years beyond the actual data; during those five years, it was assumed that a yield of 12,000 metric tons would be taken annually. Each analysis included a bootstrap with 1,000 trials.

This example is not intended as, and should not be considered to be, a formal assessment of the swordfish fishery. Such an assessment would normally include additional information and analysis, including age-structured population models and numerous sensitivity analyses. Also, the abundance index used here was developed solely to serve an example, and is not believed to be an accurate reflection of abundance over time.

The North Atlantic swordfish fishery enjoyed a high catch rate in 1962 and 1963, but it declined in the late 1960s (Fig. 1). The U.S. and Canadian portions of the fishery were sharply reduced in the early 1970s because of FDA regulations prohibiting interstate transportation or importation of fish with mercury concentrations exceeding the allowable level of 0.5 ppm (Hoey et al., 1989). In 1978, the FDA increased the allowable mercury content to 1 ppm, and since then, the catch has increased, but the CPUE has slowly declined (Fig. 1B). For the years 1971–73, early years of the FDA regulations, data are available on catch but not on fishing effort.

Results from the two analyses were similar, but they illustrate how tuning can influence the results of a production model. In each analysis, the model fits the effort data reasonably well (Fig. 2); however, because the hypothetical abundance index does not match the observed CPUE well (Fig. 1B), the fit in the last years of the tuned model was a compromise

between matching the observed effort (Fig. 2B) and matching the index (Fig. 2C). The tuned analysis gave lower estimates of MSY, f_{MSY}, and a less optimistic impression of the current level of the stock, as represented by the ratio B_{1992}/B_{MSY} (Table 2). It also estimated that the recent fishing mortality rate, as represented by the ratio F_{1991}/F_{MSY}, was somewhat higher.

Estimated median biases from each analysis were small. In the base analysis, no management benchmark was estimated to have a bias exceeding 1.5% of the corresponding uncorrected estimate (Table 2). Estimated median biases for the tuned analysis were only slightly higher; with only the estimated bias in f_{MSY} slightly exceeding 2%. Estimates of median bias in individual model parameters (such as r and K) were slightly higher yet, but only for B_1 was bias estimated as higher than about 2.5%.

Table 1

Data used in two production model analyses loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean. Yield and standardized fishing-effort-rate data are from Hoey et al. (1993) with minor revisions. Hypothetical abundance index data are the mean of ages 3 through 5+ in numbers from Scott et al. (1992). The index was constructed solely for illustrative purposes, and is designated "hypothetical" because it probably is not a good indicator of total-stock biomass.

Year	Yield (t)	Fishing effort rate (10^6 hooks/yr)	Hypothetical abundance index
1962	5,342	6.45	—
1963	10,189	8.54	—
1964	11,258	24.45	—
1965	8,652	25.30	—
1966	9,338	31.39	—
1967	9,084	28.90	—
1968	9,137	40.11	—
1969	9,138	43.23	—
1970	9,425	38.47	—
1971	5,198	—	—
1972	4,727	—	—
1973	6,001	—	—
1974	6,301	19.22	—
1975	8,776	22.97	—
1076	6,587	21.17	—
1977	6,352	18.14	—
1978	11,797	20.40	—
1979	11,859	40.13	—
1980	13,527	35.44	—
1981	11,126	34.85	1.000
1982	12,832	40.73	0.816
1983	14,423	55.10	0.488
1984	12,516	49.44	0.483
1985	14,255	59.55	0.526
1986	18,278	80.75	0.411
1987	19,959	98.91	0.377
1988	19,137	97.08	0.368
1989	17,008	90.46	0.359
1990	15,594	85.86	0.352
1991	13,212	69.86	—

Approximate 80% nonparametric confidence intervals computed by Equations 14 and 15 were derived from the bootstrap. These were computed for the individual model parameters, management benchmarks, indicators of stock position, and for each year's relative stock size estimate (Table 2; Fig. 3). A unitless nonparametric measure of the precision of estimates was constructed by dividing the bias–corrected 50% confidence interval (interquartile range; not shown here) by the corresponding median bias–corrected estimate. The resulting statistic, the relative interquartile range (RIR) is a nonparametric analog of the coefficient of variation. The RIR was of similar magnitude for both models, and was smallest in MSY and f_{MSY}, the benchmarks that do not depend on q. Estimates of the quantities that depend on q, and that thus involve absolute scaling, exhibited relative IQ ranges of about 50% (Table 2).

Estimates of relative biomass (B_τ scaled to B_{MSY}) and fishing mortality rate (F_τ scaled to F_{MSY}) were also similar from the two models (Fig. 3). They show a declining biomass through 1991, with an increase expected thereafter (at the projected harvest rate of 12,000 t/yr, which is less than the MSY estimates). As expected, the precision of estimates during the projection period was less than during the period for which data were available.

In summary, this example demonstrates that much more than MSY can be estimated from a production model. Biomass trajectories can be computed easily, as can estimated confidence intervals derived through the bootstrap. If an independent index of abundance is available, the model can be tuned to that index. Another useful feature is that projections can be used to estimate the probable effects of quotas or other management measures.

Discussion

The modeling framework described here is based on the logistic population model. The history of this model was summarized by Kingsland (1982), who pointed out that the model originated in the work of Verhulst (1845) and Robertson (1923), was popularized by Pearl and Reed (1920), and was also studied by Lotka (1924). The model was introduced to fishery science by Graham (1935) and Schaefer (1954,

1957). In modeling fish populations, one could just as easily use the exponential yield model of Fox (1970) or a model of more flexible shape, such as that of Pella and Tomlinson (1969) or its alternative formulation by Fletcher (1982). (Fletcher's formulation lacks the estimated exponent that has been found to complicate estimation [Ricker 1975, p. 326].) Unfortunately, those formulations can not supply an analytical formulation similar to Equations 6 and 8, which means that numerical integration would have to be used, as in the GENPROD computer program of Pella and Tomlinson (1969). Another alternative would be to use a discrete-time model, rather than the continuous-time model presented here. Such models are simpler mathematically, but usually entail assumptions that the growth, recruitment, and catching seasons are brief. The logistic model was used here because it is a simple case, not because using other models would be impractical or inferior.

For what types of stocks are the models presented here appropriate? Research is lacking to answer this question definitively, but general comments are possible. One group of fishes for which production models seem to work well is the tropical tunas. These species are characterized by relatively fast growth, relatively constant recruitment, and reduced annual seasonality in the life processes. Density dependence in growth has been demonstrated in a related species, *Scomber japonicus* (Prager and MacCall, 1988); such plasticity in growth would allow the compensation inherent in a production model to be expressed in a way beyond recruitment variability. For modeling fish stocks with more seasonality in growth, reproduction, and harvest, a discrete-time production model might prove superior to the continuous-time model presented here.

In many fish stocks, recruitment is extremely variable. Ordinary production models may not work well when applied to stocks with large recruitment fluctuations that are unrelated to population size, especially when the catch–effort series is short. If recruitment fluctuations can be linked to external factors (such as variation in rainfall or sea–surface temperature), a production model incorporating these factors might work well (Freon, 1986). It would be simple to modify the logistic model to incorporate an environmental factor, perhaps as an influence on r on an annual basis.

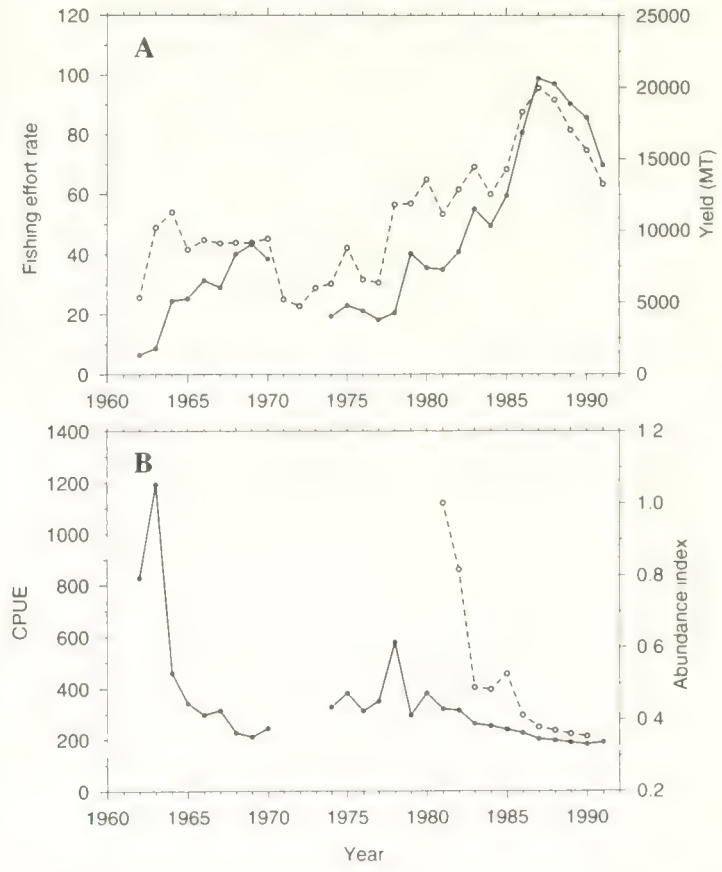

Figure 1

Data used to fit production model examples loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean. (**A**) Standardized effort rate (•) and total yield (○). (**B**) CPUE trajectory (•) computed from data in (A), and index of abundance (○) used to tune the second example. The index, which was used for illustrative purposes only, is not a good measure of total-stock abundance.

Other extensions

Many other extensions to the production model have been published. An incomplete list includes these: Fox (1975, 1977) presented a logistic production model with mixing of two stocks; Deriso (1980) and Hilborn (1990) demonstrated different methods of fitting production models to age-structured populations (but see also Ludwig and Walters, 1985); Freon (1986) introduced environmental variables into a production model that used the equilibrium assumption; Laloë (1989) and Die et al. (1990) incorporated fished area into production models; Polovina (1989) demonstrated a system of production models in which some parameters are common among models; and Hoenig and Warren (1990) demonstrated Bayesian

and empirical Bayes methods for fitting production models. Most of the extensions described by these investigators could be combined with techniques presented here (e.g. tuning, bootstrapping), as required for a particular analysis.

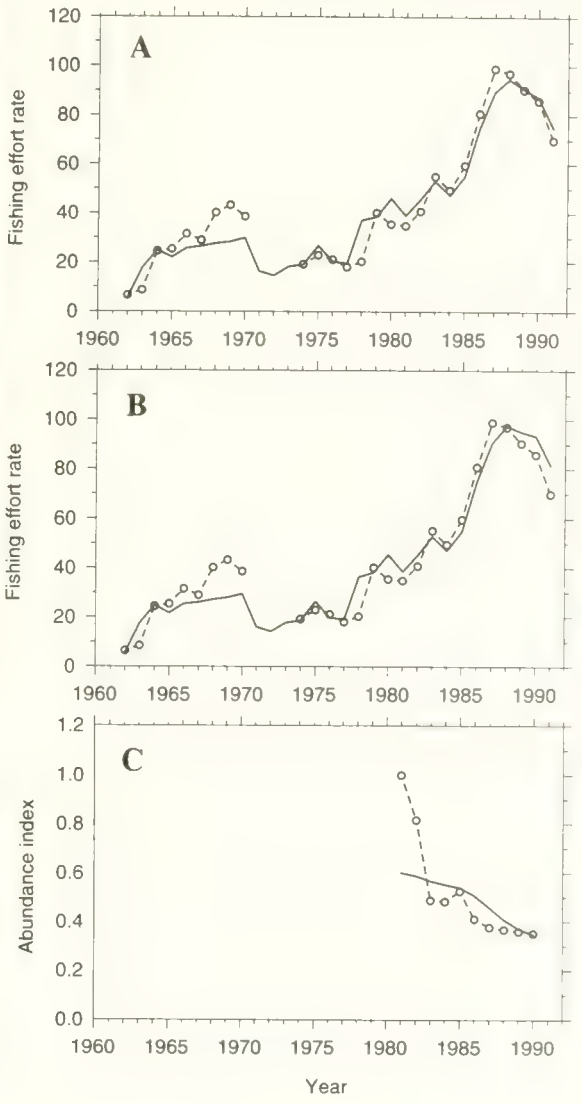

Figure 2

Goodness-of-fit of two production model analyses loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean. These analyses are illustrative and are not intended as an assessment of swordfish. Model 2 differs from Model 1 in being tuned to a hypothetical index of abundance. (**A**) Observed (o) and estimated (——) fishing effort rate from Model 1. (**B**) Observed (o) and estimated (——) effort rate from Model 2. (**C**) Observed (o) and estimated abundance-index from Model 2.

Autocorrelation

Because catch and effort data are usually autocorrelated, the residuals from fitting—whether computed in yield or effort—may also be autocorrelated. A matter of statistical concern is whether a method of fitting that takes the autocorrelation into account (such as one based on time-series analysis sensu Box and Jenkins [1976]) might be more appropriate. Some results relevant to this question were obtained by Ludwig et al. (1988) in a study that used two different objective functions to fit production models to simulated data. The first was a total-least-squares objective function, which did not take autocorrelation into account; the second, an approximate-likelihood objective function, which did. Ludwig et al. (1988) found that the two methods produced very similar estimates; the authors concluded that the added complexity of the approximate-likelihood method was probably not warranted. In addition, the approximate-likelihood method frequently failed to converge from poor starting values. This does not mean that autocorrelation should be ignored in all fisheries modeling; however, it was not a major concern in the study cited.

Process error

The model presented here assumes that the production of biomass is a deterministic function of the current biomass; stochasticity occurs only in the observation of catch or effort or in the relation of fishing effort to fishing mortality rate (if effort is being estimated from catch). In reality, production is undoubtedly stochastic to some degree. In recognition of this, fisheries models that explicitly incorporate process error have been developed (e.g. Ludwig et al., 1988; Sullivan, 1992). Because process errors are propagated forward in time, it would seem that time-series fisheries models (e.g. production models), should include corrections for process errors, so that the system can be modeled as correctly as possible.

Despite the undeniable logic of including process error in fisheries models, there are also negative aspects, and the practical merit of including process error in fisheries applications remains a topic for research. The theory of models including process error was largely developed in process control (Kalman, 1960), a field in which large data sets are common. Including both observation error and process error in a model generally entails either estimating a large number of nuisance parameters (the process errors), making strong assumptions about the form or value of the process error component, or both. In some cases, the need to estimate additional parameters can make it difficult or impossible to estimate parameters of interest, such as MSY, without additional

Table 2

Results of two bootstrapped production model analyses loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean. The base model used only yield and standardized effort data. The tuned model also used a hypothetical index of abundance (Table 1). Each conventional parameter estimate is designated $\hat{\theta}$, the corresponding bias-corrected estimate is designated $\hat{\theta}_{BC}$. Nonparametric bias-corrected 80% confidence intervals are derived from the bootstrap; as with most fishery analyses, these are conditional on correct model structure and probably underestimate true uncertainty (see text). The relative interquartile (IQ) range, a unitless measure of precision, is the 50% confidence interval divided by the median bias-corrected estimate. All results are rounded to three significant digits.

	Base model					Tuned model				
Quantity estimated	$\hat{\theta}$	$\hat{\theta}_{BC}$	80% lower CL	80% upper CL	Relative IQ range	$\hat{\theta}$	$\hat{\theta}_{BC}$	80% lower CL	80% upper CL	Relative IQ range
Management benchmarks										
MSY	13,800	13,700	11,800	15,100	11.8%	13,400	13,400	11,700	14,900	11.7%
F_{MSY}	0.257	0.259	0.161	0.393	45.3%	0.264	0.269	0.169	0.432	50.9%
f_{MSY}	72.6	71.1	61.7	82.2	14.5%	68.7	68.3	0.590	0.781	14.1%
B_{MSY}	53,800	53,100	37,400	79,700	40.7%	50,900	50,000	33,600	71,900	39.6%
B_{1992}/B_{MSY}	0.932	0.929	0.755	1.17	21.8%	0.829	0.820	0.650	1.01	23.6%
F_{1991}/F_{MSY}	1.03	1.03	0.750	1.32	28.3%	1.18	1.18	0.892	1.53	29.3%
Directly estimated parameters										
r	0.514	0.517	0.323	0.785	45.3%	0.528	0.537	0.337	0.865	50.9%
K	108,000	106,000	74,800	159,000	40.7%	102,000	100,000	67,200	144,000	39.6%
q	0.00354	0.00363	0.00236	0.00541	43.3%	0.00384	0.00393	0.00260	0.00612	45.7%

information or assumptions. (For an example, see Conser et al., 1992, and Prager, 1993). This would not be a serious objection if estimates made by models without process error were known to be severely flawed, but to my knowledge the fisheries literature includes no comprehensive comparisons of equivalent models with and without process error.

The work by Ludwig et al. (1988) does shed some light on this question, as their simulations and models included both types of error. The authors found that when observation error was ignored (its variance assumed to be zero) during parameter estimation, the resulting estimates were biased and resulted in an average loss in harvest value of at least 20%. In contrast, when the relative variance of the process error component was assumed to be half of its correct value, a substantially smaller loss in harvest value resulted. Unfortunately, Ludwig et al. (1988) did not present results for estimation under the assumption that process error was zero. Further research into estimation methods for systems with both process error and observation error would allow fishery scientists and managers to better balance complexity and accuracy in population models.

Precision of estimates

Production models tend to estimate some quantities much more precisely than others. Hilborn and Walters (1992) discuss this phenomenon at some length; the comments here reflect my own experiences. For most stocks, the main biological reference points (MSY, f_{MSY}) are estimated relatively precisely. However, absolute levels of stock biomass B_τ and fishing mortality rate F_τ are usually estimated much less precisely. This occurs because very few data sets contain sufficient information to estimate q well. (The example illustrates this point well—Table 2.) By dividing biomass and fishing–mortality estimates by estimates of the corresponding biological reference points, the effects of imprecision in estimating q can be removed. The relative levels thus obtained are useful measures in their own right: the relative level of biomass $\hat{B}_\tau / \hat{B}_{MSY}$ describes whether a population is above or below the level at which MSY can be obtained, and the relative level of fishing mortality rate $\hat{F}_\tau / \hat{F}_{MSY}$ suggests whether an increase or decrease in fishing effort might provide a higher sustainable yield.

When two or more catchability coefficients are estimated, ratios of catchability coefficients are typically estimated more precisely than the individual values of q. Thus it is possible to compare two different gears without being able to estimate very precisely the catchability of either one. If a parameterization involving K and r is used in fitting, the estimates of these quantities are usually quite impre-

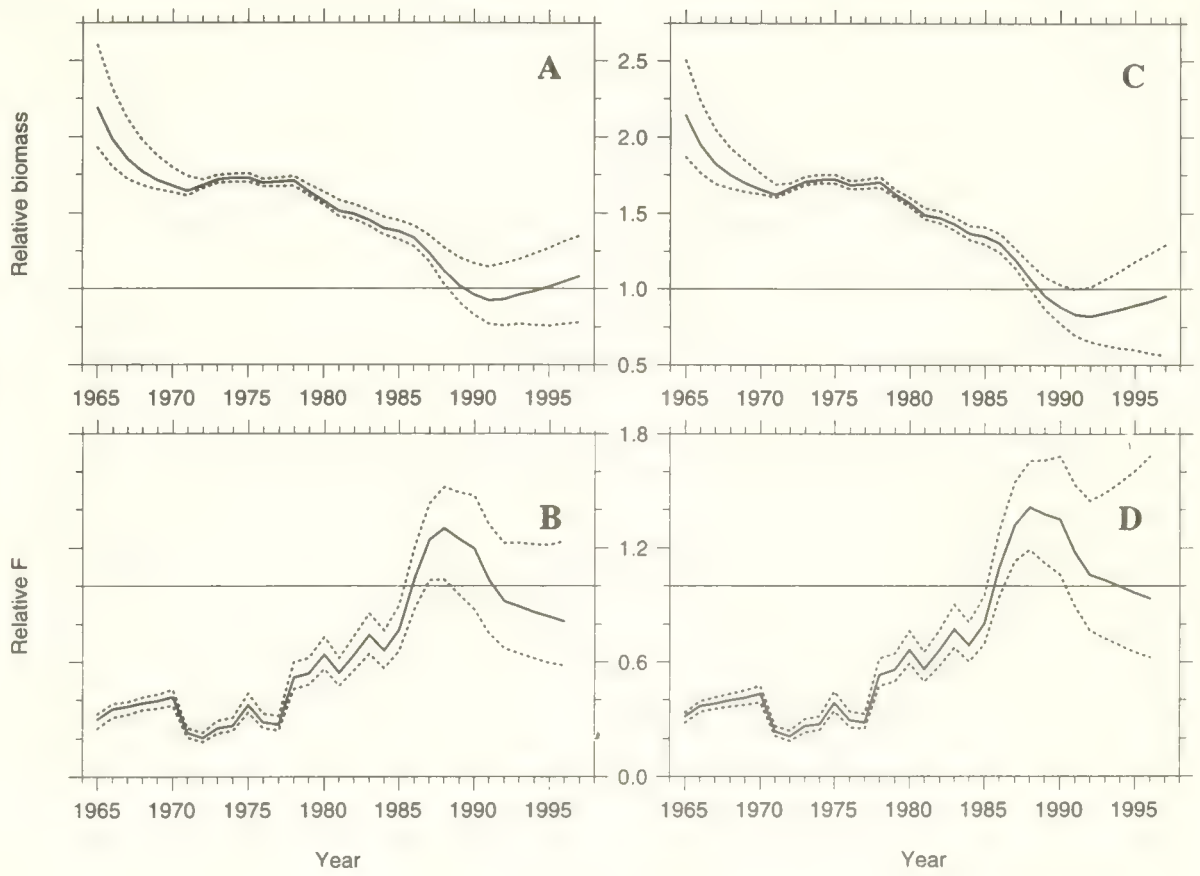

Figure 3

Estimated trajectories of relative biomass and relative fishing mortality rate from two production model analyses (including proposed yields from 1992 through 1996) loosely based on swordfish, *Xiphias gladius*, in the North Atlantic Ocean. These analyses are illustrative and are not intended as an assessment of swordfish. "Relative biomass" is the stock biomass divided by B_{MSY}, the biomass at which maximum sustainable yield (MSY) can be obtained; "relative fishing mortality rate" is the fishing mortality rate (F) divided by the rate (F_{MSY}) that yields MSY when the stock is at B_{MSY}. Production models estimate these relative quantities more precisely than the corresponding absolute quantities. Trajectories (——) are shown with approximate 80% confidence intervals (---) from the bootstrap. Model 2 differs from Model 1 in being tuned to a hypothetical index of abundance. Panels (**A**) and (**B**), estimates from Model 1; (**C**) and (**D**), estimates from Model 2.

cise, but because they are correlated, the corresponding estimates of MSY and optimum effort can nonetheless be quite precise.

The estimate of B_1, the starting biomass in the first year, is usually quite imprecise even when normalized to B_{MSY}. It is also my impression that it can be biased for some data sets, although this does not significantly affect relative biomass estimates beyond the first few years. I would therefore not recommend using a production model to draw any inferences about the population biomass during the first few (perhaps 2 to 4) years, unless auxiliary information is available. Such information might comprise a biomass index (for tuning) or knowledge to support using an assumption of the type $B_1 = sK$, where s is a proportionality constant known a priori. Punt, 1990, provides an example. This indeterminacy in production modeling is similar to the inability of sequential population (age-structured) analyses to say much about population dynamics in the most recent years unless auxiliary information is used. In practice, it does not seem to degrade the estimates of MSY and optimum effort when a reasonably long time series is used.

Validity of bias corrections and confidence intervals

Bootstrap confidence intervals are approximations, and bias-correction methods can at times worsen the

approximation. DiCiccio and Tibshirani (1987) demonstrate an example in which "the BC and BC_a methods seem to pull the percentile interval in the wrong direction and hence the coverage gets worse." (The BC_a method, due to Efron [1987], incorporates a second-order correction to the BC method.) In that example, bias correction for the point estimate would also have made it worse. The example presented by DiCiccio and Tibshirani (1987) (estimating the variance of a correlation coefficient, true value 0.9, from a data set of 15 observations) seems rather extreme, but it does serve to emphasize that model results, including estimated bias corrections, must not be accepted blindly.

Confidence intervals estimated by bootstrap methods entail fewer assumptions than those made by parametric methods, but most likely are still optimistic. In a study of an econometrics equation (including a lagged term) that was fit by generalized least squares with an estimated covariance matrix, Freedman and Peters (1984) found the bootstrap estimates of standard error far superior to those made with asymptotic assumptions. The bootstrap estimates were 20% to 30% too low, but estimates from asymptotic formulas were too low by factors of almost three. One reason for underestimation by the bootstrap was that, due to the effect of fitting, the residuals used for resampling were smaller than the true values of the disturbance term (Freedman and Peters, 1984). A suggested correction is given by Stine, 1990, p. 338.

There are other reasons why estimated confidence intervals for fisheries models are likely to be optimistic. The time frame encompassed by the data used to fit fisheries models is usually short and does not encompass the full range of environmental variation that can add unexplained variation to observed data. As the time series becomes longer, the random effects of environmental variation tend to become more extreme, making earlier confidence intervals appear overly optimistic (Steele and Henderson, 1984). Another cause of optimistic confidence intervals is the use of preliminary models (e.g. ANOVA) to construct abundance indices; such models tend to filter the indices and thus reduce apparent variance. There may also be systematic errors in the data (from, e.g. gradual changes in q or gradual or sudden changes in the proportion of the catch reported); these can bias the results, but the confidence intervals include only the effects of variability, not bias from model misspecification. Schenker (1985) stated that "bootstrap confidence intervals should be used with caution in complex problems." It is probably appropriate to consider estimated confidence intervals from fisheries population models to be, in general, minimum estimates.

Is there life after death?

The concept of maximum sustainable yield was given its epitaph about 15 years ago in a critical review by Larkin (1977). Notwithstanding the title of his paper, Larkin's main target was not the concept of MSY itself, but what he called the "religion" of applying MSY dogmatically to every stock. Undoubtedly, one must recognize that MSY is not an immutable quantity, and that model results should not be used dogmatically. However, compensation in population dynamics does give rise to some form of maximum sustainable yield. Whether MSY is estimable from the data available for a given stock, and whether it is a useful concept given the stock's dynamics, are reasonable questions that, even if answered in the negative, do not invalidate the concept of MSY.

In a response to Larkin's (1977) paper, Barber (1988) pointed out that MSY, far from being dead, was still in widespread use. Barber cited the utility of MSY as a formal management objective; its simplicity and ability to be understood by the fishing industry, administrators, and managers; and the grounding of the MSY concept in basic ecological theory. He concluded by repeating Holt's (1981) suggestion that MSY be considered part of a multi–faceted management scheme.

Shortly following Larkin's (1977) paper, Sissenwine (1978) discussed several shortcomings of MSY as the basis for optimum yield (OY), the "legally mandated immediate objective of marine fisheries management in the coastal waters of the United States beyond the territorial sea of the individual states." In this section, I address those items not discussed earlier. Sissenwine pointed out that it is difficult to estimate q, and that q may vary with population size. This difficulty might be overcome, to some degree, by the methods described earlier for estimating changes in q. More importantly, this problem is not unique to production models. The common use of CPUE series to tune age-structured models also requires strong assumptions about q. Indeed, because an age-structured model generally provides little information about a cohort before it has been substantially fished, its estimate of population biomass in a year close to the present may be more influenced by random variations in q than would a similar estimate from a production model.

Sissenwine (1978) made a number of criticisms of production models fit by equilibrium assumption. The methods described here do not use the equilibrium assumption and are not subject to those problems. Once the assumption is dropped, one is much less likely to get a good, but spurious, fit, when modeling a population whose dynamics are not approximated

by the model. This is an excellent reason (but not the only one) to avoid the equilibrium assumption.

A final important point raised by Sissenwine (1978) is that, because the world is stochastic, one is truly more interested in maximum average yield (MAY) than MSY. Several studies (Doubleday, 1976; May et al., 1978; Sissenwine, 1978) have shown that in general MAY < MSY; thus harvesting MSY indefinitely would lead to stock collapse. This result does not make production models less useful, but does emphasize the necessity to use their results in the context of other knowledge about the stock and as part of an evolving view of stock dynamics. Fishery assessment and management are dynamic processes that must adapt to changing conditions and new knowledge. It is inconceivable that we will ever know enough about any wild stock to establish a management regime that could be effective into the indefinite future. The failure of MSY to be such a regime is no failure at all.

Notes added in proof

1 I have recently been made aware of several production-model applications that were circulated in the Collected Papers of the International Commission on Southeast Atlantic Fisheries (ICSEAF). Pertinent documents include those by Butterworth et al., 1986; Andrew et al., 1989; and Punt, 1989.

2 Anyone attempting to implement the methods described here should be aware that Equation 6, when solved for F, can be double-valued.

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Literature cited

Barber, W. E.
1988. Maximum sustainable yield lives on. N. Am. J. Fish. Manage. 8:153–157.

Box, G. E. P., and G. M. Jenkins.
1976. Time series analysis: forecasting and control, revised ed. Holden-Day, San Francisco.

Conser, R., J. M. Porter, and J. J. Hoey.
1992. Casting the Shepherd stock-production model in a statistical framework suitable for swordfish stock assessment and management advice. Int. Comm. Cons. Atl. Tunas (Madrid), Coll. Vol. Sci. Pap. 39:593–599.

Deriso, R. B.
1980. Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. 37:268–282.

Deriso, R. B., T. J. Quinn II, and P. R. Neal.
1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42:815–824.

DiCiccio, T., and R. Tibshirani.
1987. Bootstrap confidence intervals and bootstrap approximations. J. Am. Stat. Assn. 82:163–170.

Die, D. J., V. R. Restrepo, and W. W. Fox Jr.
1990. Equilibrium production models that incorporate fished area. Trans. Am. Fish. Soc. 119:445–454.

Doubleday, W. C.
1976. Environmental fluctuations and fisheries management. Int. Comm. Northw. Atl. Fish., Sel. Pap. 1:141–150.

Efron, B.
1982. The jackknife, the bootstrap, and other resampling plans. Society for Industrial and Applied Mathematics, Philadelphia, 92 p.
1987. Better bootstrap confidence intervals. J. Am. Stat. Assn. 82:171–200.

Efron, B., and G. Gong.
1983. A leisurely look at the bootstrap, the jackknife, and cross-validation. Am. Statistician 37:36–48.

Efron, B., and R. Tibshirani.
1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Stat. Sci. 1:54–75.

Fletcher, R. I.
1982. A class of nonlinear productivity equations from fishery science and a new formulation. Math. Biosci. 61:279–293.

Fox, W. W., Jr.
1970. An exponential yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99:80–88.
1975. An overview of production modeling. Int. Comm. Cons. Atl. Tunas (Madrid), Coll. Vol. Sci. Pap. 3:142–156.
1977. Some effects of stock mixing on management decisions. Int. Comm. Whal. Rep. 27:277–279.

Freedman, D. A., and S. C. Peters.
1984. Bootstrapping a regression equation: some empirical results. J. Am. Stat. Assn. 79:97–106.

Freon, P.
1986. Introduction of environmental variables into global production models. Proc. Int. Symp. Long Term Changes Mar. Fish Pop., Vigo (Spain), p. 481–528.

Gavaris, S.
1988. An adaptive framework for the estimation of population size. Can. Atl. Fish. Sci. Adv. Comm., Res. Doc. 88/29.

Graham, M.
1935. Modern theory of exploiting a fishery, and application to North Sea trawling. J. Cons. Int. Explor. Mer 10:264–274.

Gulland, J. A.
1975. The stability of fish stocks. J. Cons. Int. Explor. Mer 37:199–204.

Hilborn, R.
1990. Estimating the parameters of full age-structured models from catch and abundance data. *In* L.-L. Low (ed.), Proceedings of the symposium on application of stock assessment techniques to gadids. Int. N. Pac. Fish. Comm. Bull. 50:207–213.

Hilborn, R., and C. J. Walters.
1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, NY, 570 p.

Hinkley, D. V.
1978. Improving the jackknife with special reference to correlation estimation. Biometrika 65:13–21.

Hoenig, J. M., and W. G. Warren.
1990. Bayesian and related approaches to fitting stock production models. ICES CM-1990/D:13, 21 p.

Hoey, J. J., R. J. Conser, and A. R. Bertolino.
1989. The western north Atlantic swordfish. *In* W. J. Chandler (ed.), Audubon wildlife report 1989/1990, p. 456–477. Academic Press, San Diego.

Hoey, J. J., J. Mejuto, J. Porter, and Y. Uozumi.
1993. A standardized biomass index of abundance for North Atlantic swordfish. Int. Comm. Cons. Atl. Tunas (Madrid), Coll. Vol. Sci. Pap. 40:344–352.

Holt, S. J.
1981. Maximum sustainable yield and its application to whaling. *In* J. Gordon Clark (ed.), Mammals in the seas, vol. 3, p.22–55. FAO Fish. Ser. 5.

Kalman, R. E.
1960. A new approach to linear filtering and prediction problems. J. Basic Eng. 82:34–45.

Kennedy, P.
1979. A guide to econometrics. MIT Press, Cambridge, MA, 175 p.

Kingsland, S.
1982. The refractory model: the logistic curve and the history of population ecology. Q. Rev. Biol. 57:29–52.

Kizner, Z. I.
1991. Bootstrap estimation of the confidence intervals of stock and TAC assessments with the use of dynamic surplus production models. NAFO Sci. Coun. Studies 16: 149–152.

Laloë, F.
1989. Un modèle global avec quantité de biomasse inaccessible dépendand de la surface de pêche. Application aux données de la pêche d'albacore (*Thunnus albacares*) de l'Atlantique Est. Aquat. Liv. Res. 2:231–239.

Larkin, P. A.
1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. 106:1–11.

Lotka, A. J.
1924. Elements of physical biology. Reprinted 1956 as "Elements of mathematical biology" by Dover Press, NY, 465 p.

Ludwig, D., and C. J. Walters.
1985. Are age-structured models appropriate for catch-effort data? Can. J. Fish. Aquat. Sci. 42:1066–1072.

Ludwig, D., C. J. Walters, and J. Cooke.
1988. Comparison of two models and two estimation methods for catch and effort data. Nat. Res. Modeling 2:457–498.

MacCall, A. D.
1976. Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse seine fishery. Calif. Coop. Ocean. Fish. Invest. Rep. 18:136–148

Marquardt, D. W.
1963. An algorithm for least squares estimation of nonlinear parameters. J. Soc. Ind. Appl. Math. 2:431–441.

May, R. M., J. R. Beddington, J. W. Horwood, and J. G. Shepherd.
1978. Exploiting natural populations in an uncertain world. Math. Biosci. 42:219–252

Methot, R. M.
1989. Synthetic estimates of historical abundance and mortality for northern anchovy. Am. Fish. Soc. Symp. 6:66–82.
1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data. *In* L.-L. Low (ed.), Proceedings of the symposium on application of stock assessment techniques to gadids, p. 259–277. ICNAF Bull. 50.

Nelder, J. A., and R. Mead.
1965. A simplex method for function minimization. Comp. J. 7:308–313.

Noreen, E. W.
1989. Computer–intensive methods for testing hypotheses: an introduction. John Wiley & Sons, NY, 229 p.

Paloheimo, J. E., and L. M. Dickie.
1964. Abundance and fishing success. Rapp. P.–v. Réun. Cons. int. Explor. Mer 155:152–163.

Parrack, M. L.
1986. A method of analyzing catches and abundance indices from a fishery. Int. Comm. Cons. Atl. Tunas (Madrid), Coll. Vol. Sci. Pap. 24:209–221.

Pearl, R., and L. J. Reed.
1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc. Nat. Acad. Sci. U.S.A. 6:275–288.

Pella, J. J.
1967. A study of methods to estimate the Schaefer model parameters with special reference to the yellowfin tuna fishery in the eastern tropical Pacific ocean. Ph.D. diss., Univ. of Washington, Seattle, 156 p.

Pella, J. J. and P. K. Tomlinson.
1969. A generalized stock production model. Bull. Inter-Am. Trop. Tuna Comm. 13:419–496.

Peterman, R. M., and G. Steer.
1981. Relation between sport-fishing catchability coefficients and salmon abundance. Trans. Am. Fish. Soc. 110:585–593.

Polovina, J. J.
1989. A system of simultaneous dynamic production and forecast models for multispecies or multiarea applications. Can. J. Fish. Aquat. Sci. 46:961–963.

Prager, M. H.
1993. A nonequilibrium production model of swordfish: data reanalysis and possible further directions. Int. Comm. Cons. Atl. Tunas (Madrid), Coll. Vol. Sci. Pap. 40:433–437.

Prager, M. H., and A. D. MacCall.
1988. Revised estimates of historical spawning biomass of the Pacific mackerel, *Scomber japonicus*. Calif. Coop. Ocean. Fish. Invest. Rep. 29:81–90.

Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling.
1986. Numerical recipes: the art of scientific computing. Cambridge Univ. Press, Cambridge, 818 p.

Punt, A. E.
1990. Is $B_1 = K$ an appropriate assumption when applying an observation error production-model estimator to catch-effort data? S. Afr. J. Mar. Sci. 9:249–259.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Rivard, D., and L. J. Bledsoe.
1978. Parameter estimation for the Pella-Tomlinson stock production model under nonequilibrium conditions. Fish. Bull. 76:523–534.

Robertson, T. B.
1923. The chemical basis of growth and senescence. J. B. Lippincott, Philadelphia.

Schaefer, M. B.
1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bull. Inter-Am. Trop. Tuna Comm. 1(2):27–56.
1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Bull. Inter-Am. Trop. Tuna Comm. 2:247–268.

Schenker, N.
1985. Qualms about bootstrap confidence intervals. J. Am. Stat. Assn. 80:360–361.

Schnute, J.
1977. Improved estimates from the Schaefer production model: theoretical considerations. J. Fish. Res. Board Can. 34:583–603.
1989. The influence of statistical error on stock assessment: illustrations from Schaefer's model. *In* R. J. Beamish and G. A. McFarlane (eds.), Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, p. 101–109. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Scott, G. P., V. R. Restrepo, and A. Bertolino.
1992. Standardized catch rates for swordfish (*Xiphias gladius*) from the U.S. longline fleet through 1990. Int. Comm. Cons. Atl. Tunas (Madrid), Coll. Vol. Sci. Pap. 39:554–571.

Seber, G. A. F., and C. J. Wild.
1989. Nonlinear regression. John Wiley & Sons, NY, 768 p.

Sissenwine, M. P.
1978. Is MSY an adequate foundation for optimum yield? Fisheries 3(6):22–42.

Steele, J. H., and E. W. Henderson.
1984. Modeling long-term fluctuations in fish stocks. Science 224:985–987.

Stine, R.
1990. An introduction to bootstrap methods: examples and ideas. *In* J. Fox and J. S. Long (eds.), Modern methods of data analysis, p. 325–373. Sage Publs., Newbury Park, CA, 446 p.

Sullivan, P. J.
1992. A Kalman filter approach to catch-at-length analysis. Biometrics 48:237–257.

Thiel, H.
1971. Principles of econometrics. John Wiley & Sons, NY, 736 p.

Verhulst, P.-F.
1845. Recherches mathématiques sur la loi d'accroissement de la population. Mem. Acad. Roy. Belg. 18:1–38.

Winters, G. H., and J. P. Wheeler.
1985. Interaction between stock area, stock abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. 42:989–998.

Experimental outplanting of juvenile queen conch, *Strombus gigas*: comparison of wild and hatchery-reared stocks

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Abstract.—Stock enhancement with hatchery-reared juvenile queen conch, *Strombus gigas* L., has been suggested as a means to rehabilitate overfished populations in Florida and the Caribbean region. A 15-month field experiment was conducted in the Bahamas to compare the survival, growth, morphology, and behavior of hatchery-reared and wild juvenile conch (85–120 mm shell length). Two experimental sites were established. Site C1 contained a resident conch population whereas few conch occurred naturally at site C2. Survival was higher for wild conch than for hatchery-reared conch. After 7 months, 28% of the original wild conch were recovered compared with only 9% of the hatchery-reared conch. Thin shells, short spines, and low burial frequency in hatchery-reared conch may have caused them to be more vulnerable to predators. In a tethering experiment, about twice as many hatchery conch were killed as wild conch, but the difference was not significant inside enclosures. Survivorship was higher at the site with resident juveniles, probably because of density-dependent protection from predation. After a period of high mortality in free-ranging conch during the first two months, tag recovery curves for both stock types reached a plateau. Also, near the end of the study, shell characteristics of wild and hatchery conch were identical as was survivorship. Analysis of movement patterns indicated that both stock types moved toward the natural population center. Although survivorship was higher at the site with resident conch, growth rates for both stock types were often lower at this site. Algal foods may have been more abundant at the site without conch because of lower grazing pressure. Athough highest mean daily growth occurred at 1.0 conch·m^{-2}, growth rates of conch enclosed at 0.5, 1.0, and 2.5 individuals·m^{-2} were not significantly different in most cases. Growth rates were higher for wild conch than for hatchery conch. In summer, free-ranging and tethered wild conch grew twice as fast as hatchery-reared conch. Success in rehabilitating depleted queen conch populations will require the release of high quality, hatchery-reared juveniles in large numbers in appropriate habitats.

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Widespread depletion of natural fishery stocks, particularly in inshore coastal and estuarine habitats, has resulted in increasing interest in enhancement and restoration of wild populations through releases of hatchery-reared individuals. Among the molluscs, relatively sedentary bivalves such as oysters, *Crassostrea* spp. (Burrell et al., 1981; Goodwin[1]), clams, *Mercenaria mercenaria* (Flagg and Malouf, 1983), mussels, *Mytilus edulis* (Dare and Edwards, 1976), and giant clams, *Tridacna* spp. (Heslinga et al., 1984; Heslinga and Watson, 1985) have been restocked most successfully. Experimental reseeding of scallops, *Argopecten* and *Patinopecten* spp. (Saito, 1984; Aoyama, 1989; Tettelbach and Wenczel, 1991) and abalone, *Haliotis* spp. (Kojima, 1981; Saito, 1984; Uki, 1984; Searcy and Salas, 1985; Tegner and Butler,1985; Tong et al., 1987; Ebert, 1989; Emmett and Jamieson, 1989) also show promise.

Queen conch, *Strombus gigas*, is one of the most important fishery species in the Caribbean region (Brownell and Stevely, 1981; Berg and Olsen, 1989), with an estimated annual value of 30 million U.S. dollars (Appeldoorn and Rodriquez, 1993). Heavy fishing for queen conch in shallow water habitats has resulted in a decline of this species throughout most of its biogeographic range (Appeldoorn et al.,1987; Appeldoorn and Rodriguez, 1993), and the U.S. fishery has been closed completely since 1986 (Berg and Olsen, 1989). Mariculture has been suggested as a way to rehabilitate queen conch populations (Berg, 1976; Siddall, 1984a; Davis et al., 1987), and research efforts during the past two decades have made it possible to culture large numbers of juvenile conch for stock enhancement (Brownell, 1977; Ballantine and Appeldoorn, 1983; Hensen, 1983; Laughlin and Weil, 1983; Cruz, 1986; Davis et al., 1987; Heyman et al., 1989; Creswell,1993; Davis, 1993). Unfortunately, field outplants of hatchery-reared stock have met with little success because of very high mortality (Appeldoorn and Ballantine, 1983; Laughlin and Weil, 1983; Appeldoorn, 1985; Marshall et al., 1993; Dalton, 1993). Also, little is known about the relative viability of wild and hatchery-reared conch.

This study uses a large-scale outplant experiment, together with enclosure and tether experiments, to compare the survival, growth, morphology, and behavior of hatchery-reared and wild juvenile conch released into a well-studied nursery

[1] Goodwin, W.F. 1981 Use of seed oysters to supplement oyster production in southern North Carolina. Report, North Carolina Division of Marine Fisheries, NCDMF - Project - 2/314-R, 109 p.

site (Stoner and Sandt, 1991, 1992). This research provides further insight into the potential for using cultured conch in a stock enhancement program, and elucidates possible limitations.

Methods and materials

Site description

During the 15–month period from March 1990 to May 1991, all field outplant, enclosure, and tether experiments were carried out at two different sites designated C1 and C2 (Fig. 1). The study sites, each a 100–m square area delineated by buoys, were located 0.8 km west of Children's Bay Cay and 5.0 km southeast of the Caribbean Marine Research Center field station on Lee Stocking Island, in the southern Exuma Cays, Bahamas (lat. 23°44.5'N, long. 76°04.4'W) (Fig. 2). A shallow sand bank is to the southwest. The two sites are in a homogeneous seagrass meadow of *Thalassia testudinum* with moderate shoot density (500–700 shoots·m^{-2}) in 3.2 m depth. Tidal currents run northwest (flood) and southeast (ebb) at velocities to 50 cm·sec^{-1} with a tidal range of approximately 1.0 m. Clear water from the Exuma Sound flows over the sites on flood tides, resulting in high underwater visibility that facilitated field experiments and recovery of tagged conch.

Site C1 was established within a well-studied queen conch nursery area that has carried as many as 500,000 individuals in densities between 0.5 and 2.0 conch·m^{-2} since at least 1984 (Wicklund et al., 1991; Stoner et al. 1993, unpubl. data). Site C1 has been the location of numerous investigations on conch mass migration (Stoner et al., 1988; Stoner 1989a), distribution (Stoner and Waite, 1990), and diet (Stoner and Waite, 1991).

Site C2 was approximately 0.3 km to the southeast of site C1 and had very few juvenile conch (< 0.05 conch·m^{-2}). In 1988, small-scale transplants in enclosures showed that young conch survived and grew at nearly identical rates at sites C1 and C2 despite the absence of wild conch at the latter (Stoner and Sandt, 1992). This suggested that certain unpopulated areas of the extensive seagrass meadows in the Exuma Cays could support outplanted conch stocks.

Density estimates were obtained by counting the conch (tagged and untagged) in as many as 20 haphazardly placed circles of 4-m radius at each site at five different times during the experiment. The purpose of these estimates was to assess the natural population of conch prior to the transplant, to exam-

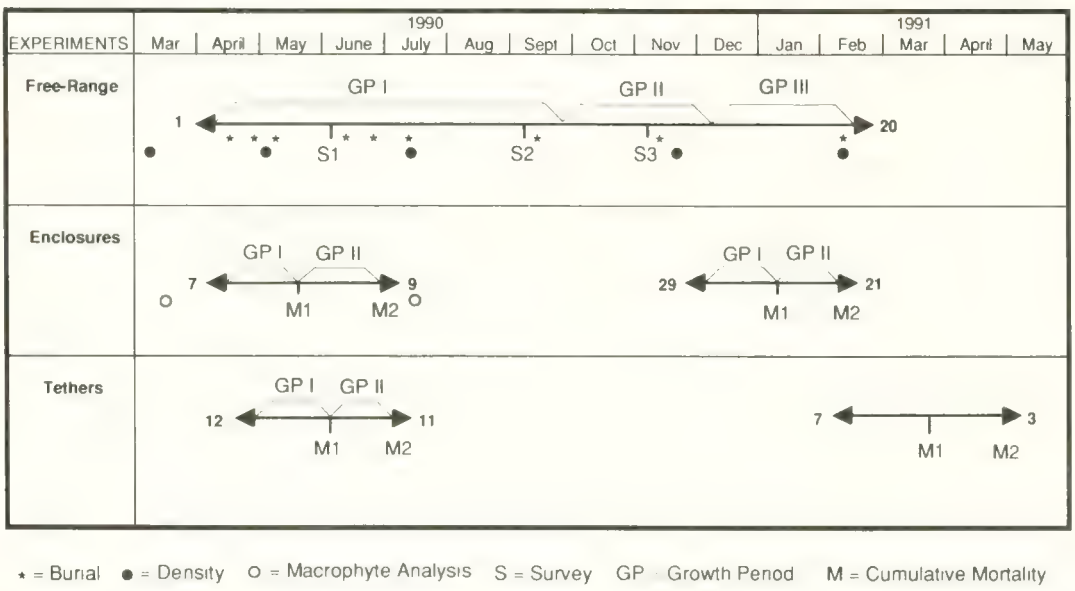

Figure 1

Calendar of free-ranging, enclosure, and tether experiments; showing duration of experiments, data collection points, and time periods for growth and mortality of queen conch, *Strombus gigas*. The total study period extended from March 1990 to May 1991. See text for descriptions of the measurements and experiments.

ine the density of conch at the end of the experiment, and to observe movements by the population. On each date up to 100 conch were measured for shell length (apex to siphonal canal).

Seawater temperature for the study site was recorded with a Ryan Temp Mentor placed on the bottom between sites C1 and C2. Temperature was recorded (+ 0.2°C) every 30 minutes, and seven-day mean temperatures were calculated for plotting (Fig. 3).

Experimental animals

Approximately 6,000 wild and 6,000 hatchery-reared conch were used in the experiments described below. Wild conch were collected from the Children's Bay Cay nursery site (C1); all were between 85 and 120 mm shell length (SL). Hatchery-reared conch were purchased from Tradewind Industries, Ltd. (Caicos Conch Farm) in Providenciales, Turks, and Caicos Islands. These conch originated from 12 egg masses collected near Providenciales in the summer of 1988. The larvae were fed with Caicos *Isochrysis* and postlarvae with flocculated *Chaetoceras gracilis* and blended *Enteromorpha* sp. (Davis et al., 1992). Between December 1988 and March 1989, 50-mm juveniles were transplanted to a protected nursery habitat near the hatchery (Davis and Dalton, 1991).

Between 26 and 29 March 1990, 6,000 hatchery-reared conch comparable in size to the 1+ year class conch native to Children's Bay Cay nursery (85–120 mm SL)(Table 1) were collected from the grow-out area and held in two 8 × 8 m holding pens. On the morning of 30 March the conch were loaded into 32 large burlap sacks wrapped in plastic bags and transported via cargo plane to Lee Stocking Island. The conch were kept cool and moist during the 7-hour period out of the water. Upon arrival, conch were immediately taken to either site C1 or C2. The plastic was removed and the burlap bags were placed on the bottom of the respective sites. On 31 March they were released into two temporary pens (10 m^2) already constructed at each of the study sites. All hatchery-reared conch were tagged and measured over the next 10 days. Wild conch were tagged and placed in temporary pens during a 10-day period prior to the arrival of the hatchery-reared conch.

All conch were marked with orange spaghetti tags (Floy Manufacturing Co.) tied around the spire, and total shell length was measured to the nearest millimeter (±1 mm) with calipers. Tags were both letter coded and numbered so that conch type and release site could be identified immediately in the field.

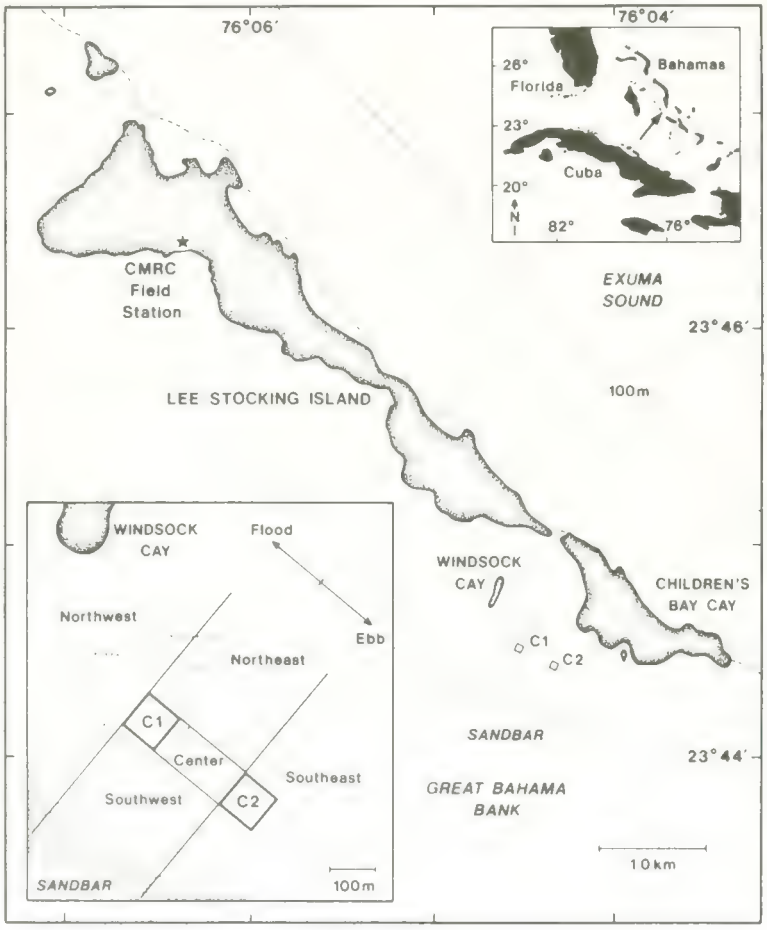

Figure 2

Map of Lee Stocking Island and Children's Bay Cay in the southern Exuma Cays, Bahamas. Study sites C1 and C2 are shown as squares, the dotted line around C1 represents the approximate boundaries of the natural queen conch, *Strombus gigas*, population in July 1990. The lower insert shows the geographic zones surveyed during each tag recovery.

Free-ranging experiment

Hatchery-reared and wild tagged conch were haphazardly released throughout each of the two 100 m × 100 m experimental sites (C1 and C2) to examine survivorship, growth, morphology, and behavior of free-ranging juveniles between 1 April 1990 and 20 February 1991. The size ranges for hatchery and

wild conch released at site C1 were 80–117 mm SL (mean=102, SD=8, n=2,552) and 85–117 mm SL (mean=100, SD=7, n=2,543), respectively. For site C2, the size ranges for hatchery and wild conch were 80–117 mm SL (mean=101, SD=8, n=2,540) and 83–117 mm SL (mean=101, SD=6, n =2,490), respectively.

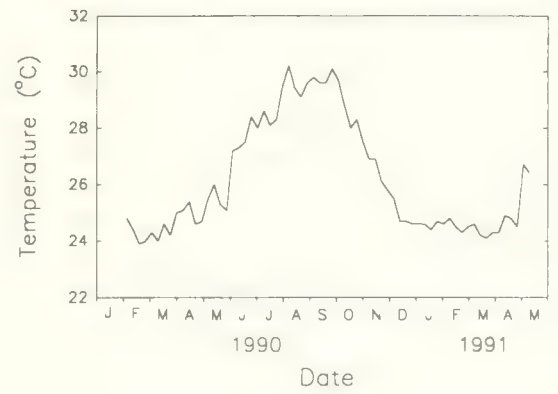

Figure 3

Bottom-water temperature recorded between sites C1 and C2, during the study period. Seven-day averages for recordings made every 30 minutes are plotted.

Table 1

Density of juvenile queen conch (*Strombus gigas*) in two field sites (C1 and C2) prior to the release of tagged conch (2 Mar. 1990), during the release experiment, and at the end of the experiment (21 Feb. 1991). Density was measured by counting conch, including tagged conch, in up to 20 randomly-selected 4-m diameter circles (50 m^2) at each site. Mean shell length for up to 100 individuals was measured for conch found in each survey. Values are mean ± SD (n).

Date	Number of plots	Density (mm)	Shell length (no./m^2)
Site C1			
2 Mar 90	20	0.26 + 0.12	105 + 14 (100)
2 May 90	20	1.27 + 1.01	n.a
16 Jul 90	20	0.66 + 0.31	111 + 12 (100)
27 Nov 90	5	0.22 + 0.12	113 + 16 (55)
21 Feb 91	6	0.19 + 0.19	129 + 13 (56)
Site C2			
2 Mar 90	20	0.01 + 0.01	99 + 14 (9)
2 May 90	20	0.03 + 0.03	n.a
16 Jul 90	20	0.62 + 0.74	119 + 10 (100)

Tag recovery Tag recapture surveys were conducted in June, September, and November 1990, to provide a relative index of survivorship over time and space. Searches encompassed the transplant sites, the zone between the sites, and adjacent seagrass and sand habitats. The search area was sectioned arbitrarily (see insert, Fig. 2), and several divers using snorkel or SCUBA gear drifted repeatedly side by side over the area using the flood tidal current for transport. Conch location was recorded by section, and searches continued until no additional conch were found. After each survey, all recaptured conch were returned to their original transplant sites (C1 or C2). Because very few hatchery-reared conch remained alive in February 1991, collections were made for shell growth and morphology, but the complete survey was not conducted.

Tag recovery does not measure absolute survivorship because of potential emigration from the study site and possible inefficiency in finding tagged animals; however, the search effort was intensive, and clear water (usually >10 m horizontal visibility) facilitated the efficiency of the searches. In two blind tests 87 and 92% of 200 uniquely tagged conch were recovered by using standard search procedure (unpubl. data). The surveys were conducted over periods from 7 to 20 days depending upon the number of divers available. Because of known limitations, tag recovery data were used as a relative indicator of survivorship in the two stock types and two study sites.

Growth Seasonal growth rates ($mm \cdot day^{-1}$) were determined for three periods: summer (April to September 1990), fall (September to November 1990), and winter (November 1990 to February 1991) by comparing shell lengths of individual, tagged conch at the beginning and end of the survey periods.

Shell morphology At the beginning (1 April 1990) and end of the experiment (20 February 1991), representative samples of at least 30 hatchery-reared and 30 wild conch (collected alive) were measured for shell length and width, and shell and tissue weight. Maximum shell width was the distance between the last complete spine formed near the shell aperture and the spine on the opposite side of the shell. Total weight of the shell and soft tissue (live weight) was recorded to the nearest 0.01 g. After freezing and subsequent thawing, the soft tissue of the animal was extracted, lightly blotted, and weighed. Weights of the clean, air-dried shells were also recorded.

Behavior Nine times during the study, observations on burial behavior were made for the first 30 hatch-

ery-reared and 30 wild conch (tagged individuals) at each outplant site. Burial frequency was quantified as the percentage of conch that had at least part of the shell buried in the sediment, detritus, or algae. Counts for the two sites were pooled for each of the conch types. General observations on locomotory activity were also recorded.

Data from the tag recovery surveys provided information on the movements of free-ranging conch. During each tag recovery the type (wild or hatchery-reared), initial site of transplant (C1 or C2), and number of tagged conch found in different regions around the initial release sites (Fig. 2) were recorded. The total number of conch found in each survey was used to calculate the percentage of hatchery or wild conch from site C1 or C2 in each area surveyed.

Enclosure experiments

Experiment I Enclosure experiments were designed to determine the significance of density-dependent growth and survival of hatchery-reared and wild conch in identical habitats. The first 3-month experiment was conducted from 7 April to 9 July 1990. At each site (C1 and C2) 12 circular pens (30 cm high, 20 m^2) without covers were constructed of vinyl coated wire mesh (2.5 × 5.0 cm). Prior to the experiment (23 February–12 March) three haphazardly placed 25 × 25 cm quadrants per cage were sampled for *Thalassia testudium* components to ensure habitat similarity among the pens, both within and between stations. In each quadrant, seagrass shoot density was estimated, and all above-ground parts were collected into 3–mm mesh nylon bags. Living blades and detritus were separated in the laboratory, dried at 80°C and weighed. Detritus measurements were made again at the end of the experiment (9–13 July 1990) to test for potential depletion of this important food source.

At each site tagged hatchery and wild conch were placed in pens at three different densities, in two random blocks. Stocking densities, spanning the high range of natural densitites in the wild, were 0.5, 1.0, and 2.5 conch·m^{-2} (10, 20, 49 conch·pen^{-1}). The size ranges for hatchery-reared and wild conch were 90–109 mm SL (mean=100, SD=3) and 92–115 mm SL (mean=102, SD=3), respectively. Before stocking the pens with experimental conch, all visible epibenthic predators such as tulip snails, *Fasciolaria tulipa*, apple murex, *Murex pomum*, and the giant hermit crab, *Petrochirus diogenes*, and sea urchins *Tripneustes esculentus* were removed. Every two weeks throughout the experiment, dead conch were replaced to ensure constant density; replacements were not used in growth and survivorship measurements.

Cumulative mortality was calculated by subtracting the number of live conch remaining from the initial loading number. Mortality was examined statistically at the midpoint (day 37) and at the end (day 93) of the experiment. Shell length was measured at the start, near the middle (day 37), and at the end (day 93) of the experiment, and growth rates were calculated for the two periods.

Experiment II A second 3-month enclosure experiment was conducted at sites C1 and C2 to compare survival and growth of hatchery-reared and wild conch in the winter (29 November 1990–21 February 1991). Enclosures built for experiment I were reused in this experiment after having been clear of conch since July 1990. Four enclosures at each site were stocked with 10 hatchery-reared and 10 wild conch (1.0 conch·m^{-2}) gathered from the surrounding free-ranging populations. This density was chosen because highest mean growth rates frequently occurred at this density in enclosure experiment I. The initial size of the hatchery-reared conch ranged from 104–130 mm SL (mean=118, SD=5) and the wild conch ranged from 109–134 mm SL (mean=122, SD=5).

Dead conch were replaced with similar sized free-ranging conch every two weeks. As in the first experiment cumulative mortality and growth rates were determined only for the original stock, not the replacements. Mortality was calculated five times throughout the experiment, and analyzed statistically at the midpoint (day 35) and end (day 84) of the experiment. Growth rates were calculated for two growth periods, 29 November 1990 to 3 January 1991 and 3 January to 21 February 1991.

Tether experiments

Experiment I The first three-month tethering experiment was conducted during the summer (12 April to 11 July 1990) at sites C1 and C2 to examine survivorship, tag effects, and growth rates. The size ranges for hatchery-reared and wild conch were 82–116 mm SL (mean=100, SD=9) and 89–115 mm SL (mean=101, SD=6), respectively. Each conch was secured to a 0.5-m long stainless steel welding rod by a 1 m length of 20-lb test monofilament line that was attached to the shell spire with a clear nylon cable tie. The tether rods were marked with uniquely numbered tags and pushed 40 cm into the substratum approximately 2 m apart. Conch were tethered in four rows of 20 individuals. Each row contained 10 hatchery-reared conch and 10 wild conch in an alternating pattern. For each type of conch, the shell of every second individual was tagged to determine potential tagging effects on conch mortality in the free-ranging experiment.

Cumulative mortality was examined by using the same procedure as enclosure experiment I. Mortality was calculated three times throughout the experiment, and analyzed statistically at the midpoint (day 45) and end (day 90) of the experiment. Growth rates were calculated for two growth periods: 12 April to 27 May and 27 May to 11 July 1990.

Experiment II The second 3-month tethering experiment was conducted during the winter (7 February–3 May 1991) at site C1. Too few of the original hatchery-reared conch remained alive to set up the experiment at the second site. Hatchery-reared conch ranged from 100 to138 mm SL (mean=116, SD=8), and wild conch were 111–133 mm SL (mean=124, SD=5). Tethers were set up as in experiment I with four replicated rows of 20 individuals (10 hatchery-reared and 10 wild conch), except the conch themselves were not tagged. The conch were checked for mortality three times during the experiment and analyzed statistically at days 42 and 84.

Because cable ties were secured behind long apical spines, escape from tether apparatus would be possible only in the event of failure in the cable tie, monofilament line, or connections. Failure appears to be unlikely because nearly all kills observed in this study were found as empty shells attached to the tether apparatus or as crushed shells within 1 m of the original location.

Data Analysis

Analysis of variance (ANOVA), following the guidelines of Day and Quinn (1989), was used extensively in the interpretation of growth and mortality data. The statistical procedures started with full model ANOVA that included all independent effects. When interactions were significant, one- or two-way ANOVAs were performed to examine the effects of site and stock type, the variables most critical in this study. For brevity, non-significant interaction terms in multiple-way ANOVAs are not addressed in the text but are reported in tables. Mortality data were normally examined at the mid-point of individual experiments and at the end.

Cochran's test was used to test for homogeneity of variances. Log and arcsine transformations of data were used in some cases to remove heteroscedasticity; these are noted in the text. Where repeated measurements were made within one experimental enclosure (i.e. growth rates determined for conch in one pen), mean growth rates in the enclosures were used as replicates rather than individual measurements to eliminate pseudoreplication (Hurlburt, 1984). Analysis of covariance (ANCOVA) was used to test for differences in morphological characteristics (shell weight, shell diameter, and tissue weight) between hatchery-reared and wild conch. Shell length was the covariate.

After release, tagged, free-ranging conch dispersed from the initial 1-ha study sites. Chi-square analysis was used to compare dispersion of the two stock types, where the distribution of tagged wild conch was used for the expected frequency in different survey zones.

Results

Conditions at the outplant sites

During the 15–month study period, bottom-water temperature ranged from 24°C in February 1990 to 30°C in late September 1991, then declined rapidly and remained between 24 and 25°C until early May, when temperature rose to 27°C (Fig. 3).

Density estimates made 1 month prior to the beginning of the free-ranging experiment (2 March 1990) showed that the density of conch at site C1 was 16 times higher than at site C2 (Table 1). Between March and May, conch density at site C1 increased to over 1.2 conch·m^{-2}, owing to immigration of the natural population. Transplanted conch from the free-ranging experiment made up 7–15% of the conch in the density estimates; however, on 2 May 1990, transplanted conch accounted for 88% of estimated density. In July, there were nearly equal densities of conch at sites C1 and C2, but in November 1990 and February 1991, densities were close to the original values first observed in March 1990. This may be due to directional changes in movement of conch (towards the northeast) during the winter, which took them away from the transplant sites C1 and C2 (see Behavior).

As expected, shell length measurements taken during the density surveys show an increase in length over time for wild conch tagged at C1 (from mean=105 ± 14 SD in March 1990 to mean=129 ± 13 SD in February 1991)(Table 1). This represents an overall growth rate of 0.07 mm·day^{-1}, similar to that measured in free-ranging tagged conch. No growth rate was calculated for C2, because density surveys yielded low numbers; however, the mean sizes appear to be comparable to those measured at site C1 (Table 1).

Handling and tag effects

Transporting hatchery-reared conch appeared to have little adverse effect on their subsequent survivorship in the field. Conch were left out of water for 7 hours, and all remained alive during the 7 days after transport while they were tagged and placed in enclosures for Experiment I.

Table 2

Mortality of tagged and untagged queen conch (*Strombus gigas*) on tethers at the two experimental sites. Ten tagged and ten untagged conch were tethered in each of four replicate blocks at each site. Values are mean percent mortality ± SD (number of dead conch).

	Mortality	
Site	Tagged	Untagged
C1	52.5 ± 12.6 (21)	45.0 ± 12.9 (18)
C2	40.0 ± 21.6 (16)	52.5 ± 9.6 (21)

In the first tethering experiment percent mortalities (arcsine-transformed) did not differ among any of the tag and site treatments (Table 2) (ANOVA, $F_{3,12}$=0.722, P =0.558 for C1; $F_{3,12}$=0.679, P =0.581 for C2).

Free-ranging experiment

Tag recovery Tag recapture rates for free-ranging juvenile conch were related to both stock type and location (Table 3, Fig. 4). Exhaustive searches in and beyond the study area recovered all visible live conch, and there is no reason to believe that hatchery conch were seen and collected by the divers less often than wild conch. In fact, wild conch had burial rates higher than hatchery conch (see Behavior); therefore, the reverse bias is more likely.

In November 1990, approximately 7.5 months after initial release, 206 of hatchery-reared conch were recovered from site C1 and 248 from C2, an overall recapture of 9% of the original release (Fig. 4). Recoveries of wild conch from sites C1 and C2 numbered 542 and 820 conch, respectively, an overall recapture rate of 28%. The highest proportion of loss occurred during the first two months (April and May 1990). After May, recovery curves for both hatchery and wild conch leveled off at both sites. Tag recapture was consistently higher for wild conch released at site C2 (34% at experiment end) than for those released at C1 (22%), despite the presence of large num-

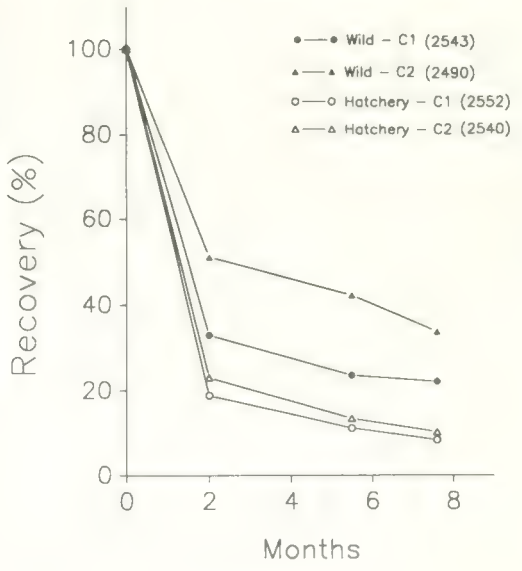

Figure 4

Recovery rates for free-ranging hatchery-reared and wild queen conch, *Strombus gigas*, transplanted to sites C1 and C2 in April 1990. Values are percentages of the original conch (April releases) found in June, September, and November surveys. In parentheses are the original numbers of tagged conch.

Table 3

Tag recovery summaries for hatchery-reared and wild queen conch (*Strombus gigas*) released in two study sites near Children's Bay Cay, Bahamas, in 1990. Adjustments to the original numbers of conch released in April account for tagged conch taken from the free-ranging study to be used in enclosure and tether experiments; these were subtracted from the original number.

	Site			
	C1		C2	
Stock type	Hatchery	Wild	Hatchery	Wild
April to June (64 days)				
Original Number Released in April	2552	2543	2540	2490
Recovered Live	480	837	586	1270
% Recovered Live	18.8	32.9	23.1	51.0
June to September (100 days)				
Adjusted Number Released	2517	2467	2472	2451
Recovered Live	277	582	328	1035
% Recovered Live	11.0	23.6	13.3	42.2
September to November (66 days)				
Adjusted Number Released	2502	2452	2457	2436
Recovered Live	206	542	248	820
% Recovered Live	8.2	22.1	10.1	33.7

bers of untagged, wild conch at the C1 area. Hatchery stocks were recovered in about equal proportions at the two sites.

Growth Free-ranging wild conch had higher growth rates (log-transformed) than hatchery-reared conch during all three seasons examined (Table 4). During summer, the difference was approximately two times (Fig. 5), but the rates began to converge in the fall. Growth rates were highest during summer and fall, and lowest during winter, following patterns of water temperature (Fig. 3). Conch grew significantly faster at site C2 than at C1 during both summer and winter; site differences were not significant in the fall (Table 4, Fig. 5).

Morphology At the beginning of the free-ranging experiment, shells of hatchery-reared conch were significantly lighter than those of wild conch from the Children's Bay Cay nursery site (slopes were homogeneous, F=0.833, P=0.365; ANCOVA: F=92.62, P< 0.001) (Fig. 6A). Lower shell weight in hatchery-reared conch is a function of either thinner shells or differences in shell form compared to wild conch. Regressions of shell width with shell length (Fig. 6B) showed that the spines were, in fact, longer in wild conch than in hatchery-reared stock (slopes were homogeneous, F=1.76, P= 0.190; ANCOVA: F=73.99, P< 0.001). Regressions of tissue wet weight with shell length show no significant difference in tissue weight between wild and hatchery-reared conch (Fig. 6C), (slopes were homogeneous, F=1.76, P=0.190; ANCOVA: F=3.24, P=0.077).

Measurements made on shells of hatchery-reared and wild conch at the end of the experiment in February 1991 show that lines for shell weight and width had converged (Fig. 7, A and B). Shell weights of hatchery-reared conch were still lighter than those of wild conch (slopes were homogeneous, F=0.189, P=0.665; ANCOVA: F=7.44, P=0.008) (Fig. 7A), but the lines were closer than in April 1990 (Fig. 6A). Stock type did not affect the relationship between shell length and shell width in February (Fig. 7B) (slopes were homogeneous, F=2.01, P=0.160; ANCOVA: F=0.957, P=0.331). Hatchery-reared conch

Table 4

Results of two-way ANOVAs for growth rates in free-ranging queen conch (*Strombus gigas*). "Site" refers to the two experimental sites C1 and C2. "Stock type" refers to hatchery-reared versus wild conch.

Source	df	MS	F	P
Period I (April to September 1990—64 days)				
Site × stock type	1	<0.001	1.205	0.273
Site	1	0.003	22.157	0.001
Stock type	1	0.045	322.407	<0.001
Error	396	<0.001		
Period II (September to November 1990—100 days)				
Site × stock type	1	<0.001	1.332	0.249
Site	1	<0.001	0.418	0.518
Stock type	1	0.004	16.967	<0.001
Error	396	<0.001		
Period III (November 1990 to February 1991—66 days)				
Site × stock type	1	<0.001	0.714	0.400
Site	1	0.001	7.541	0.007
Stock type	1	0.001	8.697	0.004
Error	115	<0.001		

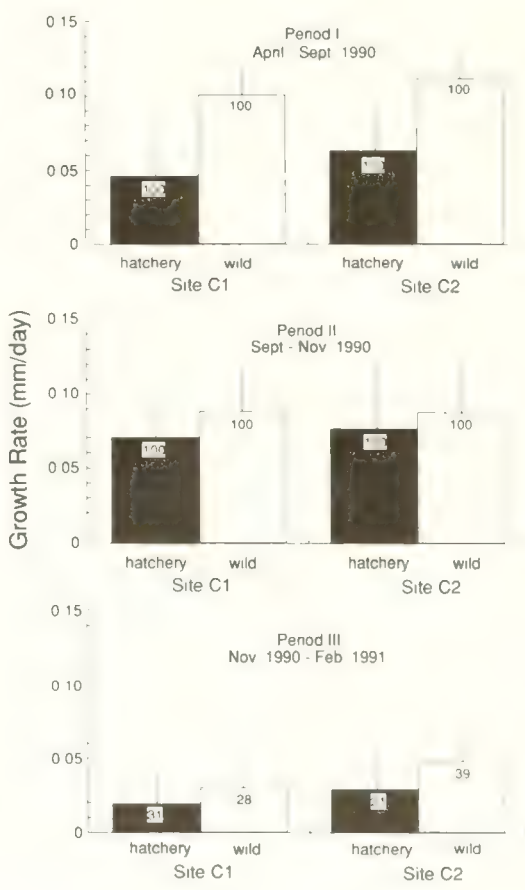

Figure 5

Comparison of growth rates of free-ranging hatchery-reared and wild queen conch, *Strombus gigas*, at sites C1 and C2. Growth periods I–III represent summer, fall, and winter, respectively. Values are mean ± SD, with the number of conch measured shown inside the vertical bars.

had heavier tissue wet weight than wild conch (slopes were homogeneous, F=0.163, P=0.688; ANCOVA: F=7.12, P= 0.010) (Fig. 7C). This can be explained by examining the ratio between tissue and shell weight. At the beginning of the experiment these ratios for hatchery and wild conch were 0.34 ± 0.04 and 0.22 ± 0.03 (mean ± SD), respectively. This indicates that hatchery conch had lighter shells and heavier soft tissue than wild conch. At the end of the experiment ratios for hatchery and wild conch were 0.30 ± 0.04 and 0.25 ± 0.04 (mean ± SD), respectively. The lower ratio for hatchery conch indicates that both the tissue and shell weight were increasing.

Hatchery-reared conch that survived 11 months in the field either developed morphological characteristics of wild conch, or the survivors had such characteristics at release. Because there was little overlap in regressions of shell width versus shell length at the beginning of the experiment, change in shape is the most plausible explanation for characteristics measured in hatchery-reared conch at the end of the experiment. Presence of short spines on pretran-

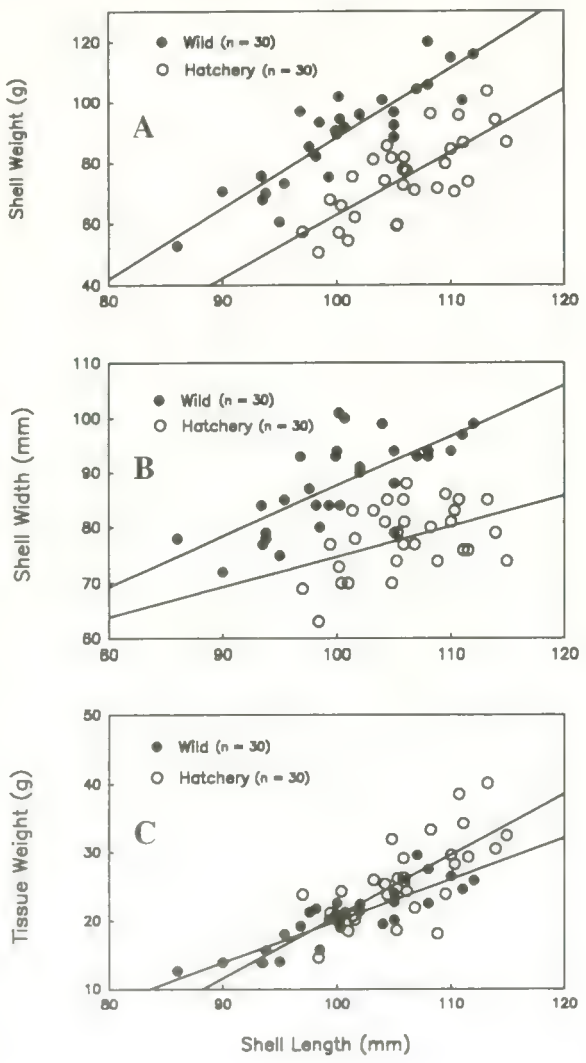

Figure 6

Shell weights (**A**), shell widths (**B**), and tissue weights (**C**) of hatchery-reared and wild queen conch, *Strombus gigas*, shown as a function of shell length. Measurements were taken for conch of each stock type collected at the beginning of the free-ranging experiment (1 April 1990).

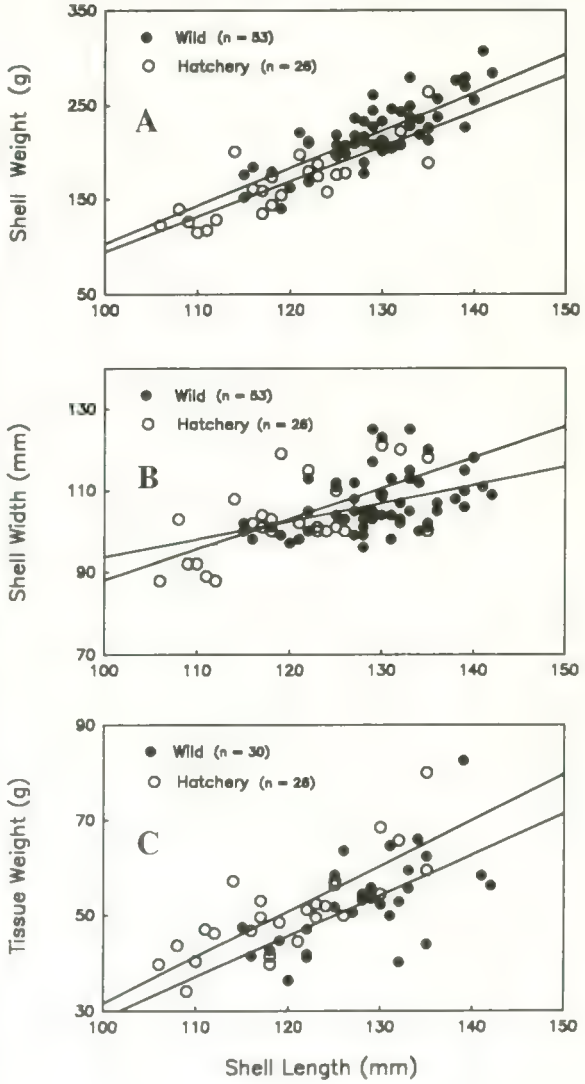

Figure 7

Shell weights (**A**), shell widths (**B**), and tissue weights (**C**) of hatchery-reared and wild queen conch, *Strombus gigas*, shown as a function of shell length. Measurements were taken for conch of each stock type collected at the termination of the free-ranging experiment (21 Feb. 1991).

splant portions of the shells followed by long spines on the outer (newer) portions of the last shell whorl support the hypothesis of changing shell shape. Although it is normal for spine length to increase proportionally with shell length in queen conch, the posttransplant increase in hatchery-reared stock was extreme and obviously disproportionate in most shells.

Behavior On all nine dates when burial was examined for free-ranging animals, a higher percentage of wild conch were buried than of hatchery-reared individuals (Fig. 8). Pairwise ANOVA of burial frequency on arcsine-transformed data from dates as blocks showed that the difference in burial rates between stock types was significant ($F_{1,15}$=8.51, P=0.011). Hatchery and wild conch showed nearly parallel patterns of burial frequency over time. However, plots of burial frequency should not be interpreted as seasonal trends, because juvenile conch appear to demonstrate tidal periodicity in locomotory activity (pers. observ.). Although the patterns were not quantified, it was frequently noted during field observations that hatchery conch were more active than wild conch. While hatchery-reared individuals were almost always moving, wild conch were frequently found nestled motionless beneath algae or detritus.

Given the relatively small area of the two outplant sites (1 ha each) tagged conch often dispersed relatively far from their original release sites (Fig. 9, A and B). For example, in June 1990 only 15% of the recovered hatchery-reared conch released at site C1 were found in that zone and 35% were found northwest of C1. Tagged conch tended to move to the northeast and northwest between April and June 1990. By June, hatchery-reared and wild conch initially released at site C1 were widely dispersed and differentially distributed (χ^2=18.01, df=4, P=0.05). Hatchery-reared conch released at C2 tended to disperse more widely than wild conch (i.e., from the southwest sandbar to the north zones); the difference was significant (χ^2=255.6, df=6, P=0.05). Wild conch moved toward the center zone between site C1 and C2 (Fig. 9B). Between June and September 1990 a large percentage of conch released at site C1 were found between C1 and C2 (Fig. 9A), while conch from site C2 continued to be found north of the release area (Fig. 9B). In both cases the difference in dispersion between hatchery and wild was significantly different (C1: χ^2=-6.4, df=5, P=0.05; C2: χ^2=17.6, df=5, P=0.05). By November 1990, hatchery and wild conch released at site C1 (χ^2=9.1, df=5, P=0.05) and C2 (χ^2=12.6, df=6, P=0.05) had similar distributions. Conch released at site C2 consistently moved toward the adjacent natural juvenile population centered at C1 (see Fig. 2).

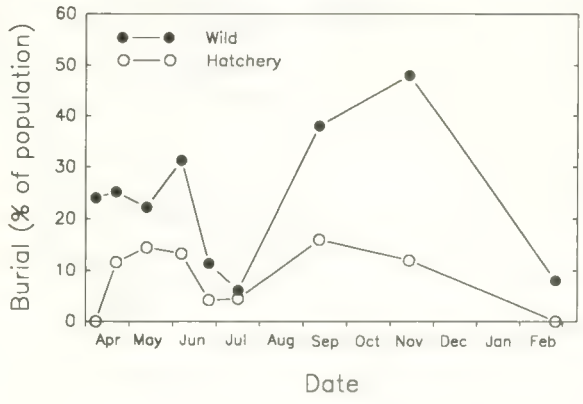

Figure 8

Percentage of queen conch, *Strombus gigas*, buried during each observation for hatchery-reared and wild conch. Values are based upon observations on 30 haphazardly chosen conch of each stock type on each date.

Enclosure experiments

Experiment I

Mortality In the first enclosure experiment (7 April to 9 July 1990), mortality data for the midpoint and end of the experiment (Fig. 10) were examined with two separate three-way ANOVAs, by using numbers of dead conch (Table 5). Except when highest mortality occured at site C2 at the end of the experiment, mortality did not differ between sites or among the three stocking densities. Differences in mortality between stock types were never significant in the enclosures (Table 5).

Growth Trends of growth (log-transformed) in the first enclosure experiment (Fig. 11) were similar to those observed in free-ranging conch during the summer (Fig. 5) (i.e. rates were higher at C2 than at C1, and wild conch grew faster than hatchery conch). In growth period I (7 April–14 May 1990), wild and hatchery conch grew faster at site C2 than at C1, and wild conch grew faster than hatchery conch at both sites (Table 6). There was also a significant density effect (Table 6); highest growth occurred in conch held at 1.0 individuals·m^{-1} (Fig. 11).

In growth period II (14 May–9 July 1990), there were numerous two-way interactions in the ANOVA (Table 6), particularly at site C1. In one-way ANOVAs, there was no density effect for hatchery ($F_{2,3}$=5.74, P=0.094) or for wild ($F_{2,3}$=7.139, P=0.072) conch at site C1; however, hatchery and wild conch

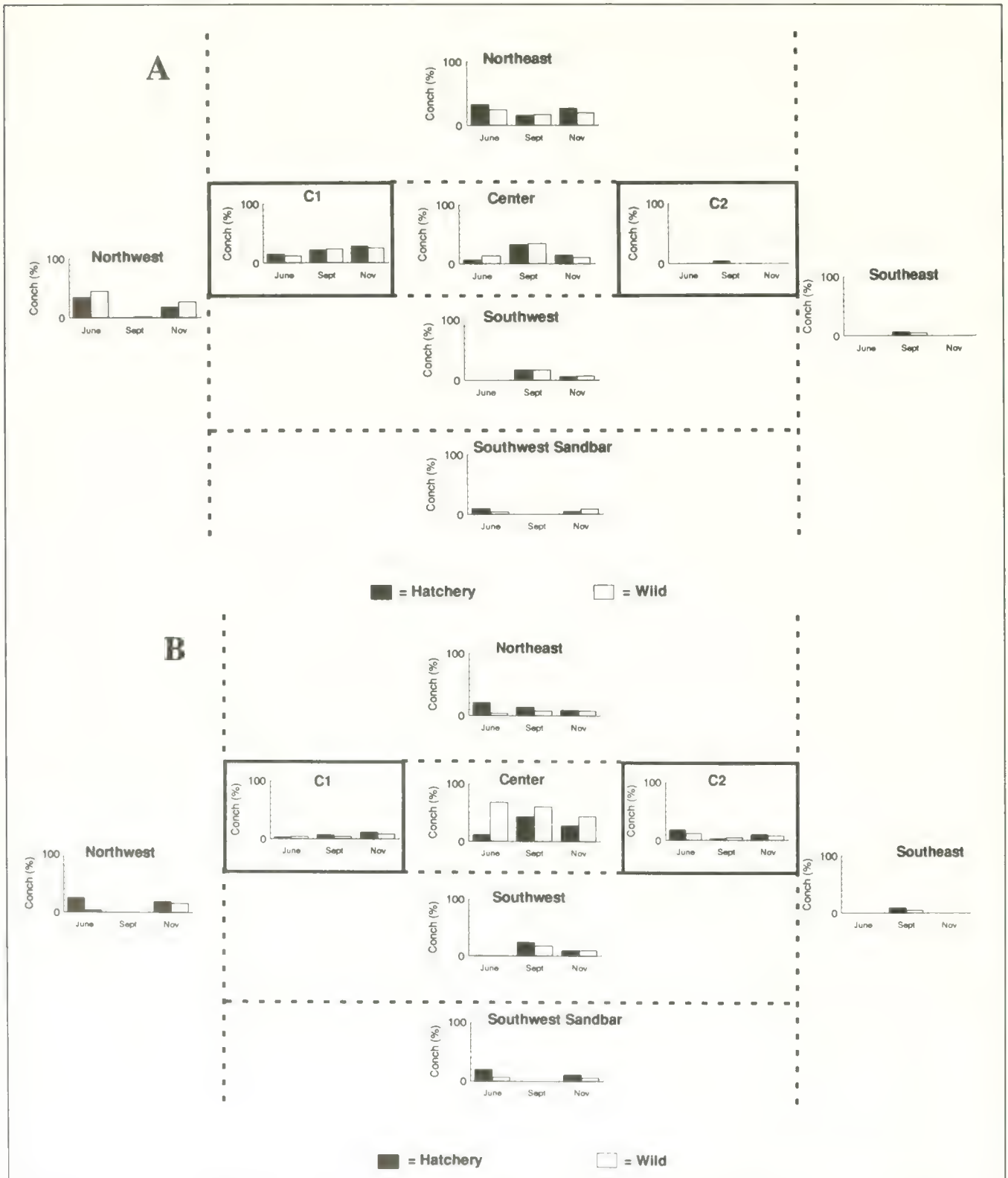

Figure 9

Recoveries of tagged queen conch, *Strombus gigas*, in the eight zones (not to scale) searched during the June, September, and November surveys. Values shown are the percentages of total capture for each stock type found in each zone, (**A**) conch released at site C1, and (**B**) conch released at site C2. See Figure 2 for true distances between the zones.

Table 5

Results of three-way ANOVAs for mortality of queen conch (*Strombus gigas*) in enclosure experiment I. "Site" refers to the two experimental sites C1 and C2. "Stock type" refers to hatchery-reared versus wild conch. "Density" is the density of conch tested in enclosures.

Source	df	MS	*F*	*P*
Period I (7 April to 14 May 1990—37 days)				
Site × type × density	2	0.015	1.266	0.317
Site × stock type	1	0.015	1.259	0.284
Site × density	2	0.003	0.258	0.777
Stock type × density	2	0.003	0.281	0.760
Site	1	0.028	2.400	0.147
Stock type	1	0.004	0.353	0.564
Density	2	0.001	0.108	0.898
Error	12	0.012		
Period II (14 May to 9 July 1990—56 days)				
Site × type × density	2	0.018	1.465	0.270
Site × stock type	1	0.010	0.839	0.378
Site × density	2	0.001	0.109	0.897
Stock type × density	2	0.018	1.447	0.273
Site	1	0.095	7.710	0.017
Stock type	1	0.008	0.691	0.422
Density	2	<0.001	0.028	0.973
Error	12	0.012		

differed in growth rate ($F_{1,10}$=10.75, P=0.008). At site C2 there were no differences in growth rate either between hatchery and wild conch or among the stocking densities (Table 6).

Prior to the beginning of the enclosure experiment, pen locations were chosen for similarity in macrophyte characteristics (Table 7). Seagrass shoot density ($F_{23,48}$=0.55, P=0.938) and macrophyte biomass ($F_{23,48}$=1.37, P=0.177) did not differ among the 24 cages. Although ANOVA showed that detritus differed ($F_{23,48}$=2.00, P=0.022) among the cages, Tukey's multiple comparison test did not detect the differences (P>0.05). At the end of the experiment dry weight of seagrass detritus did not differ among the cages (Table 7)($F_{23,24}$=0.900, P=0.598), and there were no differences in individual cages between the beginning and end of the experiment ($F_{1,142}$=0.090, P=0.764). There is no evidence, therefore, that detritus was depleted even at the high density of 2.5 conch·m^{-2}. When comparing shoot density between the beginning and end of the experiment, there was no difference ($F_{1,142}$=2.95, P=0.088), but biomass of living seagrass did differ between the dates ($F_{1,142}$=37.01, P<0.001), probably related to blade growth in the spring season.

Experiment II

Mortality At the termination (day 85) of enclosure experiment II (29 November 1990–21 February 1991) mortality was obviously higher at site C2 than at C1 for both hatchery and wild conch (Fig. 12), similar to the results of enclosure experiment I (Fig. 10). Midway through the experiment there was no significant mortality difference between site C1 and C2; however, the difference was significant by the end of the experiment (Table 8); mortality was higher at site C2. Similar to enclosure experiment I, there were no differences in mortality between hatchery and wild conch (Table 8).

Growth Growth rates were low in enclosure experiment II (0.01–0.06 mm·d^{-1}) (Fig. 13), paralleling the trend observed in free-ranging conch (Fig. 4) and associated with low winter temperatures (Fig. 3). There were significant site × stock type interactions for period I ($F_{1,12}$=5.949, P=0.031) and period II ($F_{1,12}$=5.004, P=0.045) because of differences in growth rate between hatchery and wild conch at site C1 (period I: $F_{1,6}$=6.48, P=0.044; period II: $F_{1,6}$=9.747, P=0.021); but not at site C2 (period I: $F_{1,6}$=0.008, P=0.932; period II: $F_{1,6}$=0.207, P=0.665). At site C1 wild conch grew approximately twice as fast as hatchery conch.

Tether experiments

Experiment I

Mortality The first tether experiment, conducted from 11 April to 11 July 1990, confirmed that the difference in tag recovery rate between hatchery-reared and wild conch was related to predation (Fig. 14). Hatchery conch were killed at a frequency approximately twice that of wild conch for day 45 and day 88 (Table 9, Fig. 14). Site effects were not significant at either midpoint or end of the experiment (Table 9, Fig. 14).

Growth Growth rates in both hatchery and wild conch on tethers were higher at site C2 than at site C1 by the end of the study period (11 July 1990) (Fig. 15). This difference also occurred in free-ranging conch (Fig. 5) and enclosure experiment I (Fig. 11). During period I (April and May 1990) there was a significant site × type interaction (Table 10) because wild conch grew faster at site C2 than C1 ($F_{1,64}$=49.28, P<0.001), and hatchery conch grew at

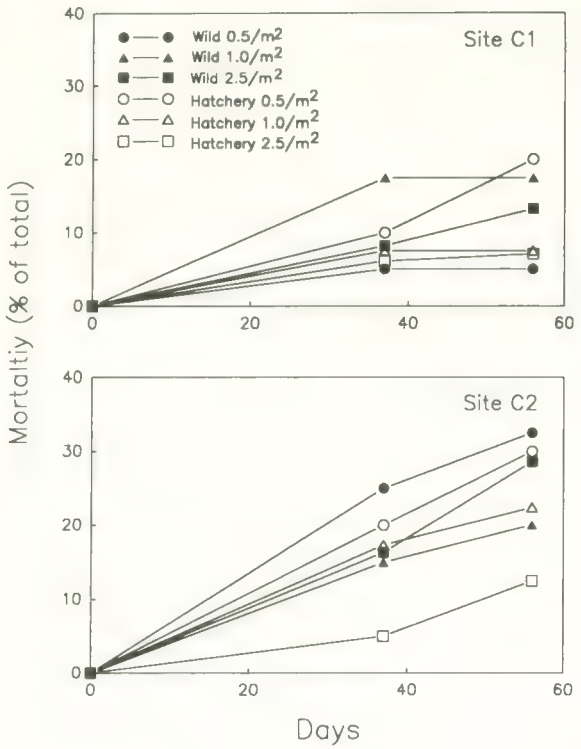

Figure 10

Cumulative mortality curves for enclosure experiment I. Hatchery-reared and wild queen conch, *Strombus gigas*, were held at three different densities at sites C1 and C2. Initial numbers of conch in the enclosures were 10, 20 and 49, yielding densities of 0.5, 1.0, and 2.5 conch·m^{-2}, respectively.

Table 6

Results of multi-way ANOVAs for growth rates of queen conch (*Strombus gigas*) in enclosure experiment I. Sources are the same as described in Table 5.

Source	df	MS	*F*	*P*
3-way ANOVA for Period I (7 April to 14 May 1990—37 days)				
Site × type × density	2	<0.001	0.481	0.630
Site × stock type	1	<0.001	0.893	0.363
Site × density	2	<0.001	2.456	0.128
Stock type × density	2	<0.001	2.284	0.144
Site	1	0.001	28.210	<0.001
Stock type	1	<0.001	16.511	0.002
Density	2	<0.001	4.649	0.032
Error	12	<0.001		
3-way ANOVA for Period II (14 May to 9 July 1990—56 days)				
Site × type × density	2	<0.001	3.546	0.062
Site × stock type	1	0.001	8.722	0.012
Site × density	2	<0.001	1.281	0.313
Stock type × density	2	<0.001	4.261	0.040
Site	1	<0.001	0.778	0.395
Stock type	1	0.0022	3.171	<0.001
Density	2	<0.001	4.787	0.030
Error	12	<0.001		
2-way ANOVA for Period II (Site C1)				
Stock type × density	2	0.001	9.513	0.014
Stock type	1	0.002	36.836	0.001
Density	2	<0.001	4.619	0.061
Error	6	<0.001		
2-way ANOVA for Period II (Site C2)				
Stock type × density	2	<0.001	0.015	0.985
Stock type	1	<0.001	1.465	0.272
Density	2	<0.001	1.935	0.225
Error	6	<0.001		

the same rate at both sites ($F_{1,43}$=0.105, P= 0.747). Wild conch grew significantly faster than hatchery conch at site C1 ($F_{1,55}$=14.54, P<0.001) and C2 ($F_{1,52}$=69.06, P<0.001) (Fig. 15). In growth period II (June and July 1990) wild conch grew faster than hatchery conch at both sites (Table 10, Fig. 15).

Experiment II A second tether experiment conducted at site C1 from 7 February to 3 May 1991, using wild conch and the few remaining hatchery-reared conch from the free-ranging experiment, resulted in mortality curves (Fig. 16) different from the first tether experiment (Fig. 14). Mortality rates did not differ between stock types at either 42 ($F_{1,6}$=0.871, P=0.387) or 84 days ($F_{1,6}$<0.001, P=1.000). Mortalities were identical (65%) at the 84–day termination of the experiment (Fig. 16).

Comparison of experiments

Mortality rates in hatchery-reared conch were higher than or equal to those of wild conch in all experiments and at both study sites (Table 11). Equivalent mortality rates were found in enclosures and in tether experiment II run at the end of the study period. Growth rates were higher in wild conch than in hatchery-reared conch except during the second 5-week period of enclosure experiment I at site C2 and in enclosure experiment II at site C2, when growth rates were equivalent.

Site differences in mortality rates were relatively consistent across experiments and stock types (Table 11). Mortality was always lower for both wild and hatchery-reared conch at site C1 than at C2, except

for equivalent mortality rates measured in tether experiment I. Most experiments showed that growth rates were lower at site C1 than at C2 with certain exceptions (Table 11). A significantly higher growth rate was found at C1 in wild conch during the second enclosure experiment, and equivalent growth rates were found in hatchery-reared conch in the same experiment. Growth rate did not differ between sites during fall in free-ranging conch.

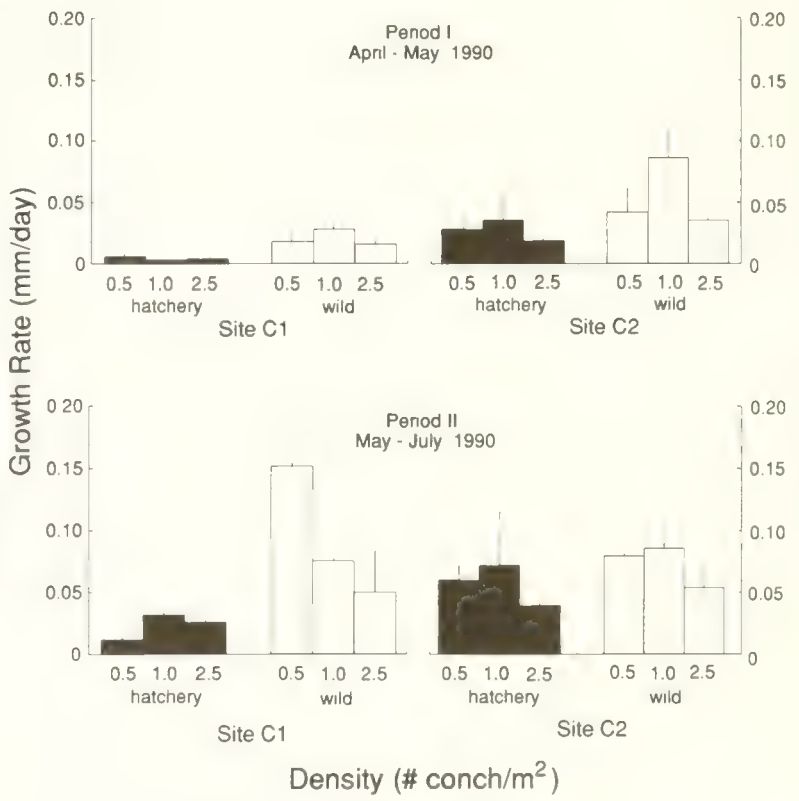

Figure 11

Growth rate comparisons for enclosure experiment I. Hatchery-reared and wild queen conch, *Strombus gigas*, were held at three different densities at sites C1 and C2. Values are mean ± SD for average growth rates in two replicate enclosures.

Discussion

Importance of seed stock quality

Stock enhancement and rehabilitation depend upon the ability of fisheries managers to place viable seed animals in optimal habitats at appropriate times (Stoner, in press). Hatcheries in the Turks and Caicos Islands, Belize, Mexico, and Florida are now producing juvenile queen conch with the expectation that hatchery-reared conch will be seeded into local waters for restoration of depleted resources. Releases of hatchery-reared conch in several small-scale pilot programs have been relatively unsuccessful in terms of conch survival (Appeldoorn and Ballantine, 1983; Appeldoorn, 1984; Iversen et al., 1986; Coulston et al., 1987; Rathier, 1987; Davis et al., 1992), but it is unknown whether low survivorship was related to characteristics of the habitat or the outplanted conch. The only published field comparison of wild and hatchery-reared queen conch (Marshall et al.[2]) showed that hatchery-reared conch may be more vulnerable to predation than are wild conch. Additionally, Jory and Iversen (1988) found that hatchery-reared conch may have shells with lower breaking strengths than those of wild conch. The present study shows that potential differences in physiology, behavior, morphology, and survival must all be considered.

Differences in growth rate between wild and hatchery-reared conch at Children's Bay Cay study sites are surprising given that the hatchery conch had been in a field grow-out enclosure with natural substrata and food for 6 months. Several explanations

Table 7

Seagrass components in 24 cages at the beginning and end of enclosure experiment I. *Thalassia* biomass included all above-ground live blades. *Thalassia* detritus included senescent and decomposing seagrass blades retained in a 3 mm mesh bag. Values are mean (± SD).

Seagrass components	March 1990	July 1990
Thalassia shoot density (shoots·m^{-2})	674.1 (±92.2)	649.3 (±79.8)
Thalassia biomass (g dry wt·m^{-2})	77.2 (±18.5)	107.2 (±37.5)
Thalassia detritus (g dry wt·m^{-2})	317.9 (±131.7)	324.32 (±25.4)

[2] Marshall, L. S., Jr., C. Cox, and R. N. Lipcius. 1992. Survival of wild and hatchery-reared juvenile queen conch in natural habitats. Unpubl. manuscr.

Table 8

Results from two-way ANOVAs for mortality of queen conch (*Strombus gigas*) in enclosure experiment II. Sources are the same as described in Table 4.

Source	df	MS	*F*	*P*
Period I (29 November 1990 to 3 January 1991—35 days)				
Site × stock type	1	0.563	0.239	0.634
Site	1	5.063	2.150	0.168
Stock type	1	0.563	0.239	0.634
Error	12	2.354		
Period II (3 January to 21 February 1991—50 days)				
Site × stock type	1	0.250	0.143	0.712
Site	1	110.250	63.000	<0.001
Stock type	1	0.250	0.143	0.712
Error	12	1.750		

Table 9

Results of two-way ANOVAs for mortality of queen conch (*Strombus gigas*) in tether experiment I. Sources are the same as described in Table 4.

Source	df	MS	*F*	*P*
Period I (12 April to 27 May 1990—45 days)				
Site × stock type	1	1.563	0.926	0.355
Site	1	0.063	0.037	0.851
Stock type	1	14.063	8.333	0.014
Error	12	1.688		
Period II (27 May to 11 July 1990—45 days)				
Site × stock type	1	<0.001	<0.001	1.000
Site	1	0.250	0.098	0.759
Stock type	1	12.250	4.820	0.049
Error	12	2.542		

Table 10

Results of two-way ANOVAs for growth rates of queen conch (*Strombus gigas*) in tether experiment I. Sources are the same as described in Table 4.

Source	df	MS	*F*	*P*
Period I (12 April to 27 May 1990—45 days)				
Site × stock type	1	0.004	28.152	<0.001
Site	1	0.005	31.072	<0.001
Stock type	1	0.014	85.104	<0.001
Error	107	<0.001		
Period II (27 May to 11 July 1990—45 days)				
Site × stock type	1	<0.001	0.535	0.467
Site	1	0.016	50.410	<0.001
Stock type	1	0.002	7.629	0.007
Error	72	<0.001		

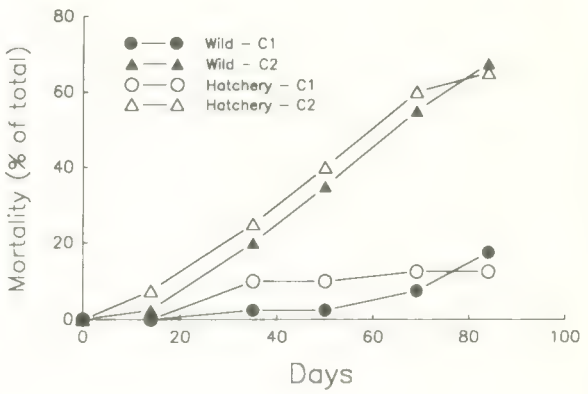

Figure 12

Cumulative mortality curves for enclosure experiment II. Hatchery-reared and wild queen conch, *Strombus gigas*, were compared at sites C1 and C2. Forty conch of each stock type were held at each site.

may be speculated: 1) hatchery and wild conch were different in their metabolic functions, such as partitioning of energy into somatic and shell growth, 2) slow growth in hatchery-reared conch was a sublethal effect of transport, or 3) poor growth was related to behavioral characteristics of hatchery-reared conch, such as a reduced ability to recognize foods in the new habitat or unusually high motility. Laboratory experiments by Siddall (1984b) showed that 10-mm juvenile queen conch held at high density had high locomotory activity and associated low growth rates. Seemingly constant motion and lack of burial in our hatchery-reared animals suggest that their metabolic demands may have been high. However, high growth rates in the hatchery conch later in our investigation showed that the problem was not a permanent characteristic of the stock type, and others have shown that hatchery-reared conch can have normal growth rates in the field (Appeldoorn and Ballantine, 1983; Davis et al., 1992). Nevertheless, as suggested earlier (Stoner and Sandt, 1991, 1992), growth appears to be a very sensitive indicator of a seed animal's physiological performance in a new habitat.

A more serious difference occurred in mortality rates. From the first field experiments with hatchery-reared queen conch juveniles (Appeldoorn and Ballantine, 1983) it has been clear that small conch are highly susceptible to predation. Recommendations for release size range from 4 cm shell length

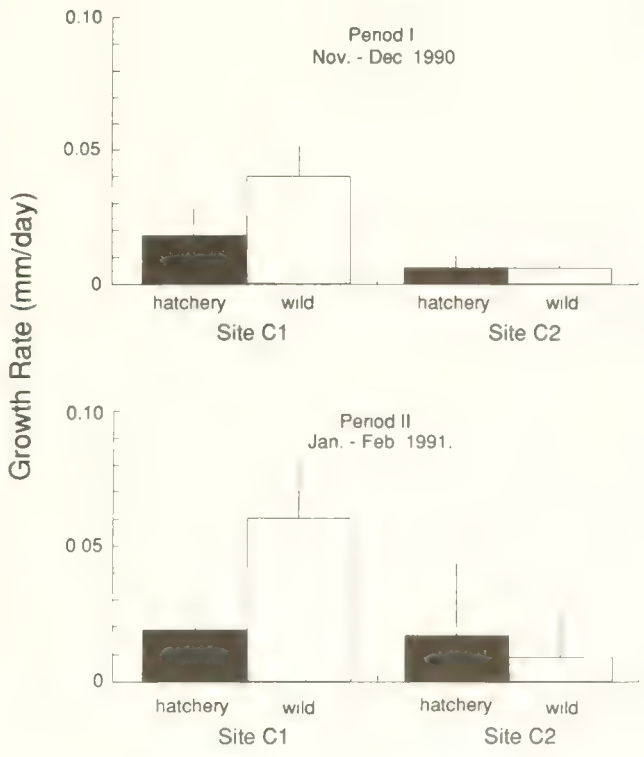

Figure 13

Growth rate comparisons for enclosure experiment II. Hatchery-reared and wild queen conch, *Strombus gigas*, were held at 1.0 conch·m^{-2} at sites C1 and C2. Values are mean ± SD for average growth rates in four replicate enclosures.

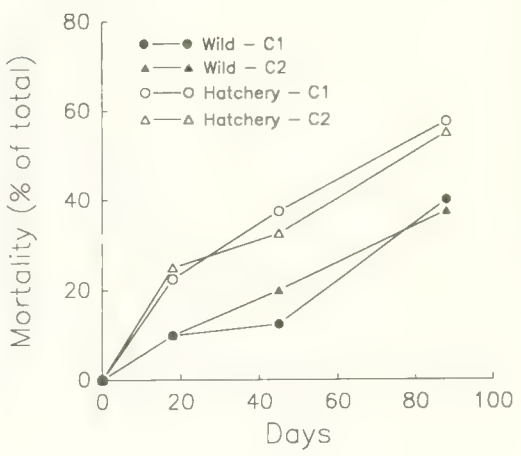

Figure 14

Cumulative mortality curves for tether experiment I. Hatchery-reared and wild queen conch, *Strombus gigas*, were compared at sites C1 and C2. Forty conch of each stock type were tethered at each site.

(Berg, 1976) to 10 cm or larger (Jory and Iversen, 1983). Even with the use of 8–12 cm shell length test animals in this investigation, hatchery-reared conch on tethers were killed at a rate nearly twice the rate of wild conch early in the study. Morphological and behavioral differences are probably the most important factors influencing mortality. Thin shells and short apical spines observed in the hatchery-reared conch would present a smaller, more vulnerable prey to predators. Palmer's (1979) experiments have shown that spination is an important shell characteristic for minimizing predation in intertidal gastropods.

Shell weight and spination are malleable traits in queen conch. Alcolado (1976) observed that shell form in the species was related to water depth and habitat type, with thin shells and short-spines being associated with rapid growth in shallow water. Environmental mediation of shell form was tested experimentally by Martin-Mora (1992) near Lee Stocking Island. She found that transplanted wild conch took on the morphology of local conch within several months, and that high shell weight and long spines were associated with slow growth rate. Given the importance of shell quality in molluscan biology, attention has been given to relationships between shell properties and diets, substrata, temperature, salinity, and other physical factors (Wilbur, 1964; Carter, 1980). It is likely, therefore, that culture techniques can be developed to provide seed conch which are less vulnerable to predation.

Survivorship of hatchery-reared conch may also have been influenced by their low burial frequency. Wild conch tend to shelter under detritus or algae, and remain partially buried and unmoving for long periods of time. This probably provides a certain degree of protection from larger visual predators. Low burial frequency in hatchery-reared conch may be related to the fact that the field grow-out area in the Caicos Islands, where they spent several months before being transplanted to the Exuma Cays, was primarily a hard-bottom environment. Behavioral differences between hatchery-reared and wild stocks are rarely documented; however, Schiel and Welden (1987) found that hatchery-reared red abalone, *Haliotis rufescens*, did not move to concealed locations as did wild abalone, resulting in higher predatory mortality.

There are at least three limitations of the present investigation. One is not knowing whether convergence in the morphology and survivorship of wild and hatchery-reared conch was related to

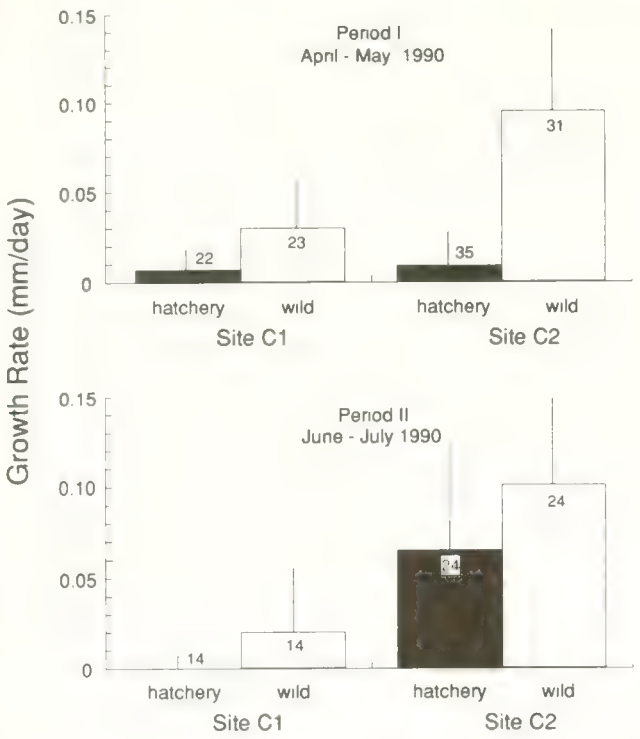

Figure 15

Growth rates of hatchery-reared and wild queen conch, *Strombus gigas*, held on tethers at sites C1 and C2 during experiment I. Values are mean ± SD, with the number of conch measured shown inside the vertical bars.

adaptation by individuals over the course of the investigation, or is explained simply by differential survivorship (i.e. the most fit hatchery-reared conch survived to the end of the experiments). As discussed earlier, a strong case for adaptation can be made because of the obvious changes in shell morphology over time within individual conch. Second, hatchery-reared conch used in this study were from one season's production in a single hatchery. We know that different hatcheries and different cultures from individual hatcheries can produce conch with different characteristics. For example, Jory and Iversen (1988) found different shell strengths among cultures of queen conch. Because juvenile conch are reared from egg masses collected from the wild, and because both shell morphology and behavior appear to be relatively plastic characteristics in queen conch, we believe that differences shown between hatchery-reared animals and native stocks can be alleviated through modifications in diets, hatchery substrata, and other culture techniques. Field viability must be considered continuously throughout the hatchery-rearing process. Third, morphological effects on survival may vary with site because of differences in predator assemblages. For example, at a site where molluscs (such as tulip snails, *Fasciolaria tulipa*) are the most important predators, size and escape behavior may be more important than spine length and shell thickness. More site comparisons and better knowledge of predator-prey relationships are needed.

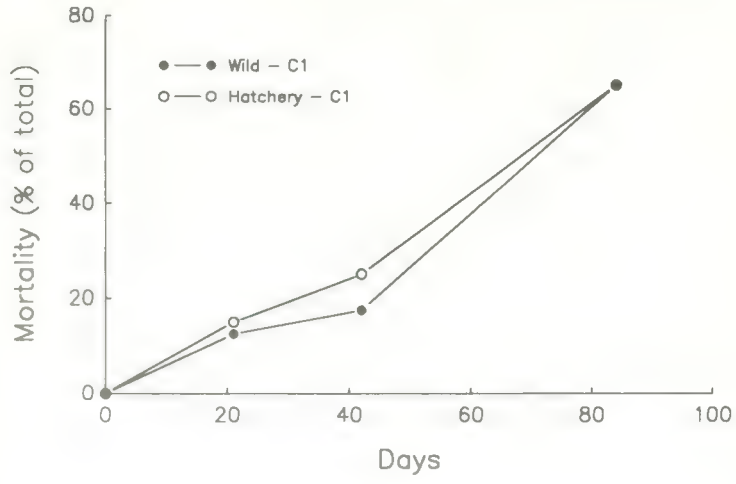

Figure 16

Cumulative mortality curves for hatchery-reared and wild queen conch, *Strombus gigas*, held on tethers at site C1 during experiment II. Forty conch of each stock type were tethered at each site.

Importance of stock enhancement sites

Site selection for stock enhancement with queen conch is a complex issue and the subject of several earlier papers (Stoner and Sandt, 1991, 1992; Stoner et al., 1993; Stoner, in press). It is clear from experiments reported here that even carefully chosen locations, such as our non-conch study site C2, may not support juvenile conch over the long term. Conch at this site demonstrated consistently higher growth than conch at the traditional nursery site (C1), but mortality was also higher in both tethered and free-ranging conch.

Site differences in mortality could be associated with patterns of predator abundance or diversity, or both. Although predators may accumulate where prey density is high, the most likely explanation for lower predation rate at site C1

Table 11

Summary of results from free-ranging, enclosure, and tether experiments on mortality and growth of hatchery-reared and wild queen conch (*Strombus gigas*) at two field sites (C1 & C2). W = wild conch. H = hatchery-reared conch. PI, PII, and PIII refer to different growth periods within the experiment. Signs indicate statistically significant differences (see text).

	Stock type		Differences	
Experiment	Site C1	Site C2	Mortality	Site differences
Free-ranging	W < H	W < H	C1 < C2	
Enclosure expt. I	W = H	W = H	C1 < C2	
Enclosure expt. II	W = H	W = H	C1 < C2	
Tether expt. I	W < H	W < H	C1 = C2	
Tether expt. II	W = H	—	—	
Growth free-ranging				
summer (PI)	W > H	W > H	W > H	W > H
fall (PII)	W > H	W > H	C1 < C2	C1 = C2
winter (PIII)	C1 < C2			
Enclosure expt. I	W > H	W > H (PI)	W = H (PII)	C1 < C2
Enclosure expt. II	W > H	W = H	W: C1 > C2	H: C1 = C2
Tether expt. I	W > H	W > H	C1 < C2	

than C2 is that juvenile conch realize density-dependent protection from predation. *Strombus* species often live in aggregations (Catterall and Poiner, 1983; Stoner et al., 1993), and recent experiments have shown that juvenile queen conch actually increase their survivorship by living in densities sufficiently high to compromise growth rate in certain cases (Stoner and Ray, 1993; Ray and Stoner, 1994). This aggregation or "herding" behavior probably reduces predation by providing a "probability refuge" (Bertram, 1978; Pulliam and Caraco, 1984); that is, the effects of predators are diluted by the presence of large numbers of alternative prey. Gregariousness provides an explanation for repeated movements of tagged conch from release site C2 toward C1, which was centered in a known juvenile aggregation. Stoner and Ray (1993) observed a similar response in queen conch translocated at another site near Lee Stocking Island. High growth rates were found outside an aggregation, but mortality was high, and movements were always toward the center of the aggregation. Regardless of the exact mechanisms involved, it is clear that both density and absolute numbers of conch released may be critical factors in an equation for success in stock enhancement. Typical nursery aggregations in the Exuma Cays range in size from less than 100,000 to several million juvenile conch (Wicklund et al.,1991; Stoner, unpubl. data). We speculate that releases at individual sites will need to be made with tens of thousands of conch; however, new research should be designed to determine the optimal number that can be released in an area, and how releases at several sites instead of just one or two might improve the probability of stock enhancement.

In this study there was no significant effect of density on growth rate over the ranges tested (0.5 and 2.5 conch·m^{-2}); however, inverse density-dependent growth was observed in another study at the same site (C1) with conch densities ranging from 1.0 to 4.0 conch·m^{-2} (Stoner, 1989b). It is not surprising therefore, that juvenile aggregations in the Exuma Cays are normally found with less than 2.0 conch·m^{-2} (Stoner et al., 1993). Such values are probably site specific. For example, at least one long-term nursery site near Lee Stocking Island rarely has more than 0.2 conch·m^{-2} (Stoner, unpubl. data). Stocking density will need to be evaluated carefully.

Different kinds of testing

General patterns of growth and mortality between the two stock types and the two outplant sites were relatively consistent among three kinds of experiments (free-ranging conch, enclosures, and tethers) (Table 11); however, the actual values measured were undoubtedly influenced by different manipulations. For example, recovery of free-ranging conch during the first two months of the experiment ranged from only 19 to 52%, whereas during the same period 70–95% survival was observed in enclosures. The coverless enclosures apparently excluded some important predators (such as the tulip snail, *Fasciolaria tulipa*),

and not all free-ranging survivors were recovered. High mortality of conch on tethers at site C2 was probably a result of the low density of conch surrounding the tethers, lack of protection provided by enclosures, and reduced ability to avoid predators. Where the density of ambient conch was high (site C1), mortality rates in enclosures and on tethers were nearly identical, suggesting the significance of alternative prey, already discussed.

Comparisons of growth rates among experimental treatments in this study are difficult to make because of different times and durations of the growth periods. For example, high growth rates in free-ranging conch calculated for April to September 1990 reflect the high temperature season. Best comparisons are provided by enclosure and tether experiments run concurrently between April and June 1990, and by growth rates for free-ranging and enclosed conch measured between December 1990 and February 1991. In both cases the conch had relatively similar growth rates within stock type and site, suggesting that caging and tethering did not affect the nutritional state of experimental animals.

Given potential artifacts of enclosures and tethers on survivorship, measurements made on free-ranging conch will be preferred for certain questions, particularly those related to behavioral patterns and natural mortality (as opposed to relative mortality measured with tethers). On the other hand, it is impossible to recover all free-ranging conch and tag recovery can not be translated directly into survivorship. Mark-recapture data can be used to estimate population changes, with certain inherent limitations (Skalski and Robson, 1992); this may be a good approach for those primarily concerned with survivorship in large outplants. Those more interested in the role of habitat, stocking densities, and mechanisms of mortality will probably wish to maintain more control over the experimental animals. Covered enclosures, such as those used by Ray and Stoner (in press), offer the best means for testing growth potential in different habitats; meanwhile tethers give good information on relative rates of mortality for comparison of different sites, conch sizes or types.

Conclusions

One of the most striking implications of Appeldoorn's (1988) estimates of natural mortality in queen conch, is that juvenile mortality is very high. For example, survivorship in the first two years of life (to approx. 130 mm SL) may be as low as 35%. Our results on recovery of free-ranging wild conch over a 7–month period corroborate Appeldoorn's calculations. One may conclude from such survivorship curves that it will take a very large number of seed conch to enhance a local stock size. The problem would be exacerbated by poor seed stock quality, releases in suboptimal habitats, or release procedures which place the conch at unusual disadvantage (e.g. poor handling and acclimation, season of release, stocking density, and seed stock size).

Success in enhancing molluscan populations with hatchery-reared stocks has been variable. For example, Tegner and Butler (1985) recovered only 1% of their outplanted red abalone, *Haliotis rufescens*, one year after release. With the same species, Ebert (1989) reported high growth coupled with modest survivorship and some individuals reached sexual maturity with ripe gonads. In Japan, considerable success has been documented with the ezo abalone, *Haliotis discus lannai* (Saito, 1984). Hatchery-reared bay scallops, *Argopecten irradians,* released into the field at 20 mm were all lost within a month in one year; however, in another year the scallops lived to reproduce (Tettelbach and Wenczel, 1991). Despite failures, success is usually achieved as a result of adequate research. Stock rehabilitation via aquaculture may be the only viable means of restoring populations depleted to near-extinction levels, as is the case for queen conch in some regions of the Caribbean (Appeldoorn et al., 1987; Berg and Olsen, 1989).

Several steps will be required for restoration of queen conch stocks in the field:

1 The quality of hatchery-reared stock must be high and consistent. Morphology, physiology, and behavior must be considered, and stock quality should be field tested before major releases. Models of the effects of hatchery stock releases on a fishery (e.g. Madenijian et al., 1991; Polovina, 1991) will be useful only if hatchery-reared and wild stocks are identical in growth and mortality.
2 Sites for releases should be chosen with respect to information on historically significant nursery grounds, and preliminary tests for habitat suitability must be run with juvenile conch of the sizes to be seeded.
3 Release techniques must be developed to optimize conch survivorship. Factors which require further research are animal size, stocking density, minimum numbers to be released, release timing (season and time of day), and animal handling and acclimation. High numbers of individuals will need to be released given natural mortality rates and success might be improved by making releases at several sites.
4 Released conch and natural stocks will need to be managed in a comprehensive, multidisciplinary

plan for the nursery habitat, considering water quality, sediments, macrophytes, and predator species, as well as the conch populations themselves.

Hatchery techniques are well developed for queen conch, but the production of high numbers of juveniles does not insure the success of stock rehabilitation programs. Success will require much basic research on the life history and ecology of the species, particularly with respect to nutrition, growth, and predator-prey interactions. A close interaction between hatchery managers, fisheries biologists, and ecologists will be key to success.

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Literature cited

Alcolado, P. M.
1976. Crecimiento, variaciones morfologicas de la concha y algunas datos biologicos del cobo *Strombus gigas* L. (Mollusca, Mesogastropoda). Acad. Cien. Cuba, Instit. Oceanol. No. 34, 36 p.

Aoyama, S.
1989. The Mutsu Bay scallop fisheries: scallop culture, stock enhancement, and resource management. *In* J. F. Caddy (ed.), Marine invertebrate fisheries: their assessment and management. Wiley & Sons, New York, p. 525–539.

Appeldoorn, R. S.
1984. The effect of size on mortality of small juvenile conchs (*Strombus gigas* Linné and *S. costatus* Gmelin). J. Shellfish Res. 4:37–43.
1985. Growth, mortality, and dispersion of juvenile, laboratory-reared conchs, *Strombus gigas* and *S. costatus*, released at an offshore site. Bull. Mar. Sci. 37:785–793.
1988. Ontogenetic changes in natural mortality rate of queen conch, *Strombus gigas* (Mollusca: Mesogastropoda). Bull. Mar. Sci. 42:159–165.

Appeldoorn, R. S., and D. L. Ballantine.
1983. Field release of cultured queen conchs in Puerto Rico: implications for stock restoration. Proc. Gulf Caribb. Fish. Inst. 35:89–98.

Appeldoorn, R. S., G. D. Dennis, and O. Monterrosa-Lopez.
1987. Review of shared demersal resources of Puerto Rico and the lesser Antilles region. *In* R. Mahon (ed.), Report and proceedings of the expert consultation on shared fishery resources of the Lesser Antilles region. FAO Fishery Report 383:36–106.

Appeldoorn, R. S., and B. Rodriguez Q. (eds.)
1993. Queen conch biology, fisheries and mariculture. Fundacion Cientifica Los Roques, Caracas, Venezuela.

Ballantine, D. L., and R. S. Appeldoorn.
1983. Queen conch culture and future prospects in Puerto Rico. Proc. Gulf Caribb. Fish. Inst. 35:57–63.

Berg, C. J., Jr.
1976. Growth of the queen conch *Strombus gigas*, with a discussion of the practicality of its mariculture. Mar. Biol. 4:191–199.

Berg, C. J., Jr., and D. A. Olsen.
1989. Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. *In* J. F. Caddy (ed.), Marine invertebrate fisheries: their assessment and management. Wiley & Sons, New York, p. 421–442.

Bertram, B. C.
1978. Living in groups: predators and prey. *In* J. R. Krebs and N. B. Davies (eds.), Behavioural ecology: an evolutionary approach. Blackwell Scientific Publ., Oxford, p. 64–96.

Brownell, W. N.
1977. Reproduction, laboratory culture, and growth of *Strombus gigas*, *S. costatus*, and *S. pugilis* in Los Roques, Venezuela. Bull. Mar. Sci. 27:668–680.

Brownell, W. N., and J. M. Stevely.
1981. The biology, fisheries, and management of the queen conch, *Strombus gigas*. Mar. Fish. Rev. 43:1–12.

Burrell, V. J., Jr., J. J. Manzi, and W. Z. Carson.
1981. Growth and mortality of two types of seed oysters from the Wando River, South Carolina. J. Shellfish Res. 1:1–7.

Carter, J. G.
1980. Environmental and biological controls of bivalve shell mineralogy and microstructure. *In* D. C. Rhoads and R. A. Lutz (eds), Skeletal growth of aquatic organisms, biological records of environmental changes. Plenum Press, New York, p. 69–113.

Catterall, C. P., and I. R. Poiner.
1983. Age- and sex-dependent patterns of aggregation in the tropical gastropod *Strombus luhuanus*. Mar. Biol. 77:171–182.

Coulston, M. L., R. W. Berey, A. C. Dempsey, and P. Odum.
1987. Assessment of the queen conch (*Strombus gigas*) population and predation studies of hatch-

ery-reared juveniles in Salt River Canyon, St. Croix, US Virgin Islands. Proc. Gulf Caribb. Fish. Inst. 38:294–306.

Creswell, L.R.
1993. An historical overview of queen conch mariculture. *In* R. S.Appeldoorn and B. Rodriquez Q. (eds.), Queen conch biology, fisheries and mariculture. Fundacion Cientifica Los Roques, Caracas, Venezuela.

Cruz, R.S.
1986. Avances en la experimentacion de produccion massiva de caracol en Quintana Roo, Mexico. Proc. Gulf Caribb. Fish. Inst. 37:12–20.

Dalton, A.
1993. Mariculture of queen conch (*Strombus gigas* L.): development of nursery and grow-out techniques. *In* R. S. Appeldoorn and B. Rodriquez Q. (eds.), Queen conch biology, fisheries and mariculture. Fundacion Cientifica Los Roques, Caracas, Venezuela.

Dare, P. J., and D. B. Edwards.
1976. Experiments on the survival, growth, and yield of relaid mussels (*Mytilus edulis*) in the Menai Straits, North Wales. J. Cons., Cons. Intern. Explor. Mer 37:16–28.

Davis, M.
1993. Mariculture techniques for queen conch (*Strombus gigas* Linné): egg mass to juvenile stage. *In* R. S. Appeldoorn and B. Rodriquez Q. (eds.), Queen conch biology, fisheries and mariculture. Fundacion Cientifica Los Roques, Caracas, Venezuela.

Davis, M., and A. Dalton.
1991. New large-scale culturing techniques for *Strombus gigas* post larvae in the Turks and Caicos Islands. Proc. Gulf Caribb. Fish. Inst. 40:257–66.

Davis, M., A. Dalton, and P. Higgs.
1992. Recent developments in conch mariculture in the Turks and Caicos Islands. Proc. Gulf Caribb. Fish. Inst. 42:397–402.

Davis, M., C. Hesse, and G. Hodgkins.
1987. Commercial hatchery procedures for queen conch, *Strombus gigas*, seed for the research and grow-out market. Proc. Gulf Caribb. Fish. Inst. 38:326–335.

Day, R. W., and G. P. Quinn.
1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59:433–463.

Ebert, T. B.
1989. Growth of hatchery reared red abalone at Fitzgerald Marine Reserve: one year post-release. Calif. Fish. Game 75:178–179.

Emmett, B., and G. S. Jamieson.
1989. An experimental transplant of northern abalone, *Haliotis kamtschatkana*, in Barkley Sound, British Columbia. Fish. Bull. 87:95–104.

Flagg, P. J., and R. E. Malouf.
1983. Experimental planting of juveniles of the hard clam *Mercenaria mercenaria* (Linné) in the waters of Long Island, New York. J. Shellfish Res. 3:19–27.

Hensen, R. R.
1983. Queen conch management and culture in the Netherlands Antilles. Proc. Gulf Carib. Fish. Inst. 35:53–56.

Heslinga, G. A., F. E. Perron, and O. Orak.
1984. Mass culture of giant clams (F. Tridacnidae) in Palau. Aquaculture 39:197–215.

Heslinga, G. A., and T. C. Watson.
1985. Recent advances in giant clam mariculture. Proc. 5th Intern. Coral Reef Symp. 5:531–538.

Heyman, W. D., R. A. Dobberteen, L. A. Urry, and A. M. Heyman.
1989. Pilot hatchery for the queen conch, *Strombus gigas*, shows potential for inexpensive and appropriate technology for larval aquaculture in the Bahamas. Aquaculture 77:277–285.

Hurlbert, S. H.
1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187–211.

Iversen, E. S., D. E. Jory, and S. P. Bannerot.
1986. Predation on queen conchs, *Strombus gigas*, in the Bahamas. Bull. Mar. Sci. 39:61–75.

Jory, D. E., and E. S. Iversen.
1983. Conch predators: not a roadblock to mariculture. Proc. Gulf Carib. Fish. Inst. 35:108–111.
1988. Shell strength of queen conch, *Strombus gigas* L.: aquaculture implications. Aqua. Fish. Manag. 19:45–51.

Kojima, H.
1981. Mortality of young Japanese black abalone, *Haliotis discus discus*, after transplantation. Bull. Jpn. Soc. Sci. Fish. 47:151–159.

Laughlin, R. A., and E. Weil M.
1983. Queen conch mariculture and restoration in the Archipelago de Los Roques. Proc. Gulf Carib. Fish. Inst. 35:64–72.

Madenijian, C.P., B.M. Johnson, and S.R. Carpenter
1991. Stocking strategies for fingerling walleyes: an individual-based model approach. Ecol. Appl. 1:280–288.

Martin-Mora E.
1992. Developmental plasticity in the shell of the queen conch *Strombus gigas*. M.S. thesis, Florida State Univ., Tallahassee, 52 p.

Palmer, A. R.
1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. Evolution 33:697–713.

Polovina, J. L.
1991. Evaluation of hatchery releases of juveniles to enhance rockfish stocks with application to Pacific ocean perch *Sebastes alutus*. Fish. Bull. 89:129–136.

Pulliam, H. R., and T. Caraco.
1984. Living in groups: is there an optimal group size? *In* J. R. Krebs and N. B. Davies (eds.), Behavioral ecology: an evolutionary approach, 2nd ed. Sinauer Assoc., Sunderland, Mass., p. 122–147.

Rathier, I.
1987. Etat d'avancement des recherches sur l'elevage du lambi (*Strombus gigas*) en Martinique. Proc. Gulf Carib. Fish. Inst. 38:336–344.

Ray, M., and A. W. Stoner.
In press. Experimental analysis of growth and survivorship in a marine gastropod aggregation: balancing growth with safety in numbers. Mar. Ecol. Prog. Ser.

Saito, K.
1984. Ocean ranching of abalones and scallops in northern Japan. Aquaculture 39:361–373.

Schiel, D. R., and B. C. Welden.
1987. Responses to predators of cultured and wild red abalone, *Haliotis rufescens*, in laboratory experiments. Aquaculture 60:173–188.

Searcy, R., and A. Salas.
1985. Studies on the ecology and re-seeding of abalone in Baja California. Trans. CIBCASIO 10:106–122.

Siddall, S. E.
1984a. Synopsis of recent research on the queen conch *Strombus gigas* Linné. J. Shellfish Res. 4:1–3.
1984b. Density-dependent levels of activity of juveniles of the queen conch *Strombus gigas* Linné. J. Shellfish Res. 4:67–74.

Skalski, J. R., and D. S. Robson.
1992. Techniques for wildlife investigations: design and analysis of capture data. Academic Press, San Diego, Calif., 237 p.

Stoner, A. W.
1989a. Winter mass migration of juvenile queen conch, *Strombus gigas*, and their influence on the benthic environment. Mar. Ecol. Prog. Ser. 56:99–104.
1989b. Density-dependent growth and the grazing effects of juvenile queen conch (*Strombus gigas* L.) in a tropical seagrass meadow. J. Exp. Mar. Bio. Ecol. 130:119–127.
In press. Significance of habitat and stock pre-testing for enhancement of natural fisheries: experimental analyses with queen conch. J. World Aquacult. Soc.

Stoner, A. W., M. D. Hanisak, N. P. Smith, and R. A. Armstrong.
1993. Large-scale distribution of queen conch nursery habitats: implications for stock enhancement. *In* R. S. Appeldoorn and B. Rodriquez Q. (eds.), Queen conch biology, fisheries and mariculture. Fundacion Cientifica Los Roques, Caracas, Venezuela.

Stoner, A. W., R. N. Lipcius, L. S. Marshall Jr., and A. T. Bardales.
1988. Synchronous emergence and mass migration in juvenile queen conch. Mar. Ecol. Prog. Ser. 49:51–55.

Stoner, A. W., and M. Ray.
1991. Experimental analysis of habitat quality for juvenile queen conch in seagrass meadows. Fish. Bull. 89:693–700.
1992. Transplanting as a test procedure before large-scale outplanting of juvenile queen conch. Proc. Gulf Caribb. Fish. Inst. 41:447–458.
1993. Aggregation dynamics in juvenile queen conch, *Strombus gigas*: population structure, mortality, growth, and migration. Mar. Biol. 116:571–582.

Stoner, A. W., and J. M. Waite.
1990. Distribution and behavior of queen conch, *Strombus gigas*, relative to seagrass standing crop. Fish. Bull. 88:573–585.
1991. Trophic biology of *Strombus gigas* in nursery habitats: diets and food sources in seagrass meadows. J. Moll. Stud. 57:451–460.

Tegner, M. J., and R. A. Butler.
1985. The survival and mortality of seeded and native red abalones, *Haliotis rufescens*, on the Palos Verdes peninsula. Calif. Fish Game 71:150–163.

Tettelbach, S. T., and P. Wenczel.
1991. Reseeding efforts and the status of bay scallop populations in New York following the appearance of brown tide. J. Shellfish Res. 10:273.

Tong, L. J., G. A. Moss, and J. Illingworth.
1987. Enhancement of a natural population of the abalone, *Haliotis iris*, using cultured larvae. Aquaculture 62:67–72.

Uki, N.
1984. Abalone culture in Japan. Proc. 9th and 10th US-Japan meetings on Aquaculture. Dep. Commer., NOAA Tech. Report NMFS 16:83–88.

Wicklund, R. I., L. J. Hepp, and G. A. Wenz.
1991. Preliminary studies on the early life history of the queen conch, *Strombus gigas*, in the Exuma Cays, Bahamas. Proc. Gulf Caribb. Fish. Inst. 40:283–298.

Wilbur, K. M.
1964. Shell formation and regeneration. *In* K. M. Wilbur and C M. Yonge (eds), Physiology of mollusca, Vol. 1. Academic Press, New York, p. 243–282.

Abstract.—A fishery for snow crab, *Chionoecetes opilio*, began in 1979 in a shallow water (<200 m) area off the Avalon Peninsula of southeastern Newfoundland and developed rapidly with landings peaking at 8609 metric tons (t) in 1981. Landings began to decline in 1982, and dropped to 74 t in 1985. This fishery collapse coincided with similar declines in catch per unit of effort (CPUE) and abundance of newly molted male snow crab. In Bonavista Bay, a deep water (>200 m) fishing area north of the Avalon Peninsula, CPUE declined less and the proportion of newly molted male snow crab remained relatively constant during the same period. Coincident with the decline of the Avalon Peninsula fishery was a pronounced drop in mean bottom temperature on the commercial fishing grounds, from –0.6° C to –1.4°C, a phenomenon not observed in Bonavista Bay. This decline in water temperature appears to have been the cause of the fishery collapse because temperatures became low enough to interrupt the molting cycle of snow crab off the Avalon Peninsula. If the potential impact of the lower water temperatures and subsequent long-term cessation of growth and recruitment within the snow crab population had been recognized, the available pool of commercial-sized crab could have been harvested more slowly over a period of years to lessen the disruption of the fishery.

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A snow crab, *Chionoecetes opilio* (Decapoda, Majidae), fishery collapse in Newfoundland

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The Newfoundland snow crab, *Chionoecetes opilio*, fishery began in 1968, and until 1978 was confined to deep water (>220 m) bays and areas within 30 km of the coast. In 1978, fishing effort in offshore areas east of the Avalon Peninsula (Fig. 1) increased markedly, resulting in peak landings in 1981 (Fig. 2) of 8609 t (Taylor and O'Keefe[1]).

The Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) recommended that annual exploitation rates for commercially harvested snow crab stocks not exceed 50–60% of annual productivity in order to prevent overexploitation (Anon.[2]). The Committee adopted this guideline because the fishery targets males only and most males have an opportunity to mate at least once before reaching the minimum legal size, thereby ensuring adequate recruitment into the fishery and the reproductive integrity of the populations. However, should there be a recruitment failure, the reproductive potential is maintained by sublegal sexually mature males in the population and females that can produce at least two clutches of viable eggs from one copulation using stored sperm (Paul, 1984).

The fishery occurs from April until November each year. Typically, catch per unit of effort (CPUE) declines throughout the fishing season until July and August when a high level of molting activity results in an increased abundance of newly molted recruits. As fishermen are discouraged by processors from landing these low-yield soft-shelled crabs, new-shelled animals of legal size (≥95 mm carapace width (CW)) generally enter the fishery in the following spring. Their recruitment is evident by high CPUE values at the beginning of the next fishing season (Taylor and O'Keefe[1]).

Between 1979 and 1982, exploitation rates off the Avalon Peninsula remained within recommended levels, but beginning in 1982 catch rates declined rapidly until 1984 when fishing became uneconomical (Taylor and O'Keefe[3]). Other areas in Newfoundland, such as Bonavista Bay (Fig. 1), have consistently had exploitation rates in excess of recommended levels and consequently have experienced reductions in catch rates. However, the

[1] Taylor, D. M., and P. G. O'Keefe. 1984a. Assessment of Newfoundland snow crab (*Chionoecetes opilio*) stocks, 1982. Can. Atl. Fish. Sci. Advis. Comm. CAFSAC Res. Doc. 84/13, Dartmouth, Nova Scotia, 35 p.

[2] Anonymous, 1981. Advice on some invertebrate and marine plant stocks. Can. Atl. Fish. Sci. Advis. Comm. CAFSAC Advisory Document 81/1, Dartmouth, Nova Scotia, 6 p.

[3] Taylor, D. M., and P. G. O'Keefe. 1986. Analysis of the snow crab, *Chionoecetes opilio*, fishery in Newfoundland for 1985. Can. Atl. Fish. Sci. Advis. Comm. CAFSAC Res. Doc. 86/57, Dartmouth, Nova Scotia, 24 p.

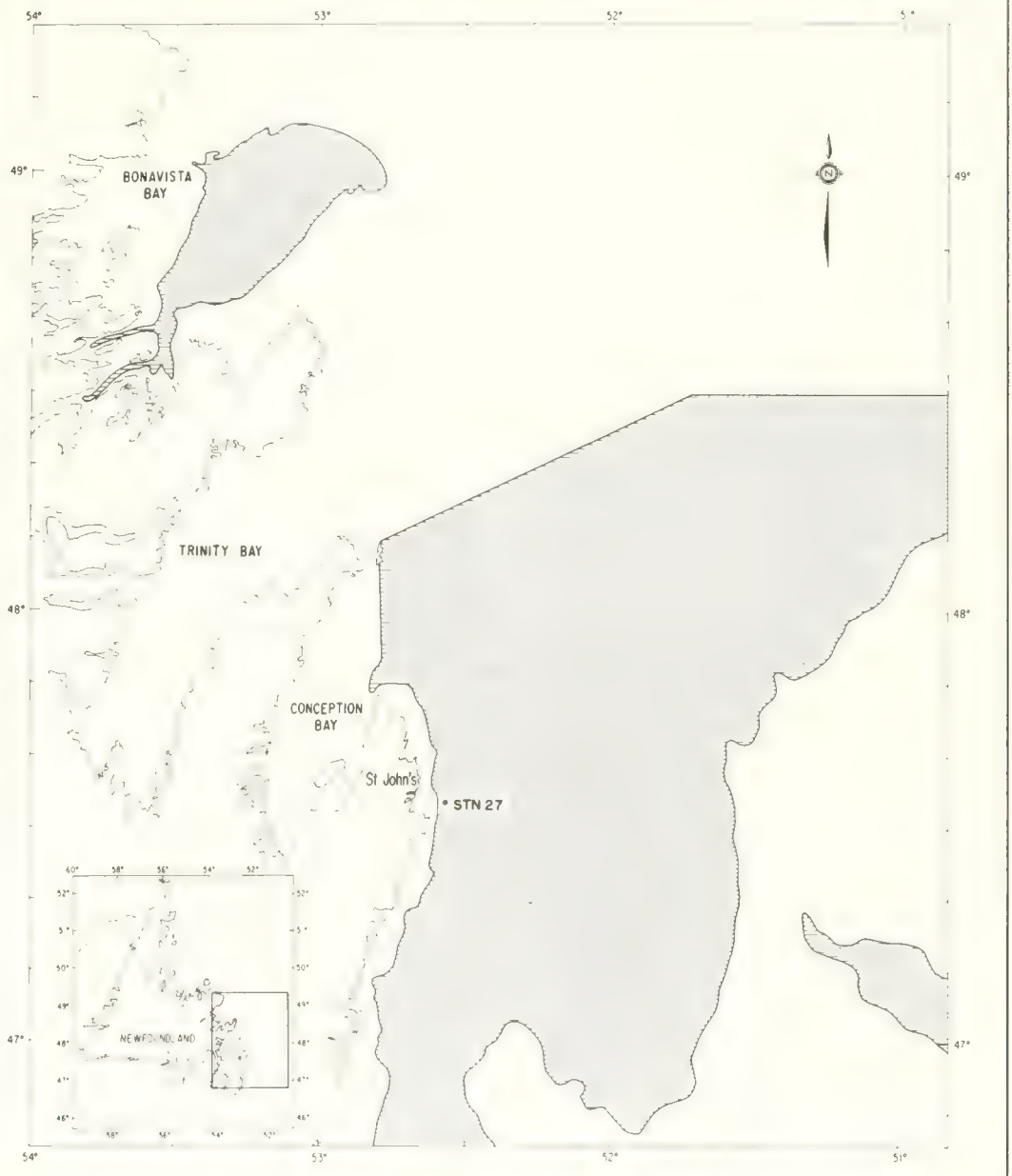

Figure 1

Offshore Avalon Peninsula and Bonavista Bay, Newfoundland, *Chionoecetes opilio* fishing grounds.

magnitude of the collapse in catch rates and landings off the Avalon Peninsula is unprecedented.

This paper examines biological data, fishermen's log returns, and temperature records from the Avalon Peninsula in comparison with similar data from Bonavista Bay in an attempt to describe possible reasons for this collapse.

Materials and methods

A total of 27 spring and fall cruises were conducted on the commercial fishing grounds off the Avalon Peninsula and in Bonavista Bay (Fig. 1) during 1979–88 to monitor population characteristics and catch rates. Fishing stations were selected randomly and strati-

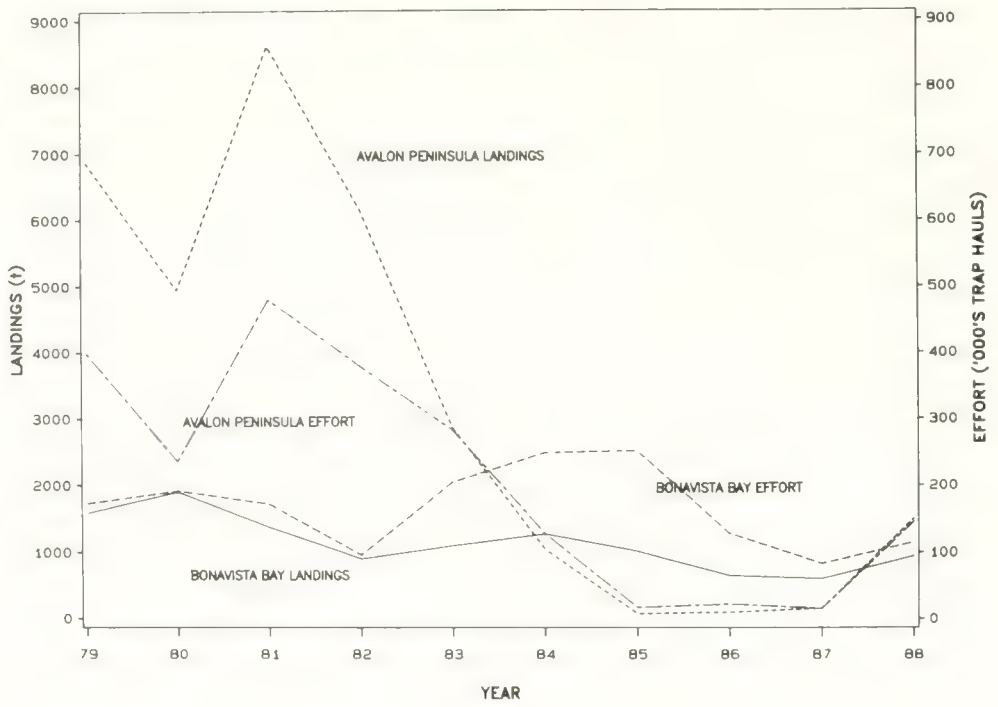

Figure 2

Summary of annual commercial landings and fishing effort for *Chionoecetes opilio* from offshore Avalon Peninsula and Bonavista Bay, Newfoundland.

fied by depth. Japanese-style conical traps baited with approximately two kg of northern shortfin squid, *Illex illecebrosus*, or with a mixture of squid and Atlantic mackerel, *Scomber scombrus*, and set in longline fleets of 12 were used to catch crabs. Although an attempt was made to duplicate the methodology employed by fishermen, space limitations onboard the research vessels restricted fleets of traps to 12 rather than the 50–70 used in commercial fishing. Weather permitting, traps were hauled after a 24–hour soak.

Crabs were removed from the traps, carapace width (CW) measured to the nearest 1 mm and shell condition determined. Three shell condition classes were used, based upon the following criteria described by Miller and O'Keefe (1981) and modified by Taylor et al. (1989):

Soft Shell (1) Carapace is brightly colored and free of epibiotic growth. Ventrally the crab is off-white to cream in color. Chelae bend, break, or crack with slight pressure. Bright iridescence present on dorsal margin of chelae. Animals within this category are considered as having molted not more than 90 days prior to capture.

New/Hard (2) Carapace is duller in color and a number of tube worms are present. Shell is hard and ventrally may be dark-cream colored and covered with discolored scratches. Chela does not bend or break when moderate thumb pressure is applied. Iridescence on chelae is reduced in intensity. This category generally applies to animals that have molted up to two years prior to capture.

Old/Hard (3) Carapace is dull brown in color and an assortment of calcareous tube worms and barnacles are present. The shell, although still hard, may have a slight "leathery" feel. Ventrally, the shell is brownish in color and many dark scratches evident. Iridescence on chelae is faint or absent. This category applies to animals that have not molted for at least two years.

Bottom temperatures from depths ≥170 m were obtained from an oceanographic station (Station 27) near the Avalon Peninsula fishing grounds (Fig. 1). There is no oceanographic station in Bonavista Bay, but bottom temperatures were obtained during eight research cruises by using expendable bathythermographs, or reversing thermometers.

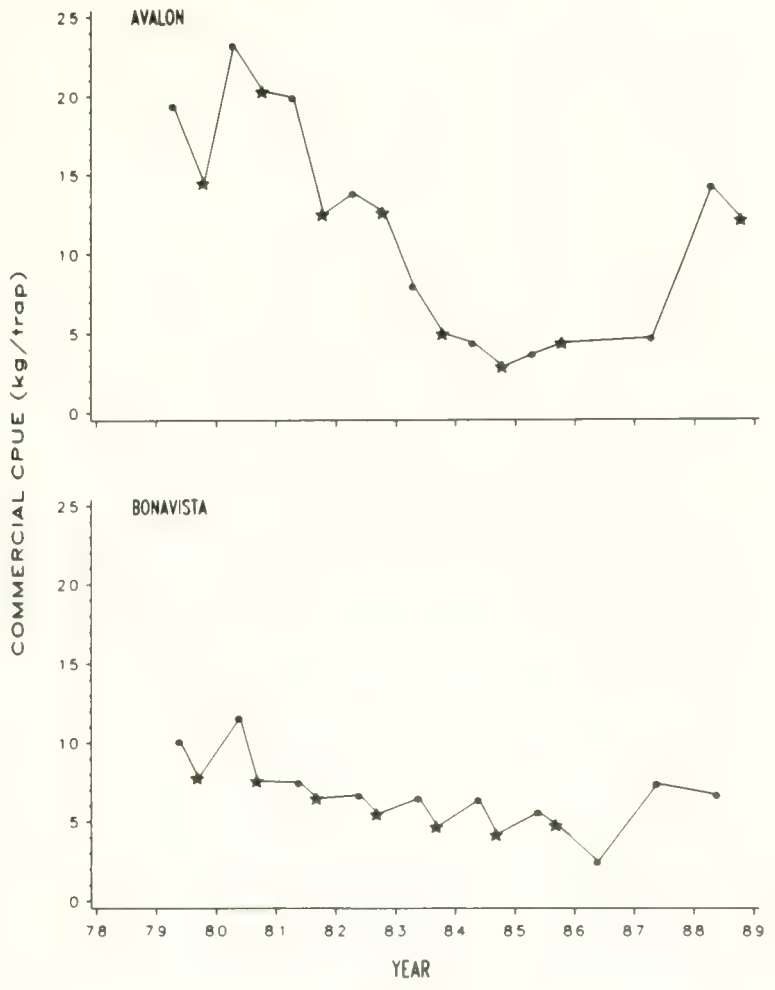

Figure 3

Commercial CPUE's for the Avalon Peninsula and Bonavista snow crab, *Chionoecetes opilio*, fisheries, 1979–88. Solid circles represent spring catch rates; stars represent fall catch rates.

CPUE's were derived for research fishing by multiplying the number of commercial crab caught per trap haul by a conversion factor of 0.45 kg/crab (Taylor, unpubl. data). Fishermen's logbook catch data were checked against processors' purchase slips. CPUE from logbook data was corrected for the percentage of sublegal crab in their catch as determined from sampling at processing plants conducted simultaneously with the research cruises. Total catch reported by log/purchase slips was then multiplied by the percentage of legal-sized animals and divided by the reported effort for the same time period to obtain a CPUE value comparable to that derived from a coincident research cruise.

Results

Logbook data

Landings and effort data from commercial logbooks are summarized in Figure 2. The drop in effort and landings for the Avalon Peninsula in 1980 is the result of a labor dispute and probably does not reflect abundance. Fishery CPUE in both the Avalon and Bonavista Bay areas was at its highest levels during the spring 1980 at 23.2 kg/trap haul and 11.6 kg/trap haul, respectively (Fig. 3). However, off the Avalon Peninsula, catch rates dropped to 19.9 kg/trap haul during the 1981 spring fishery as landings peaked at approximately 8500 t. CPUE declined to 13.8 kg/trap haul in 1982 despite logbook reports that new commercial fishing grounds were being exploited in the offshore areas (>100 km from land). This decline continued, reaching 3.7 kg/trap haul in the spring fishery of 1985 (Fig. 3), a drop of 84% from 1980 levels. This decline in CPUE was accompanied by a dramatic reduction in effort falling from 480,000 trap hauls in 1981 to 17,000 in 1985 (Fig. 2).

In comparison, the commercial spring fishery in Bonavista Bay, although overexploited (Taylor and O'Keefe[4]), has maintained a comparatively stable level of landings and CPUE since 1981 (905–1805 t and 4.1–to 8.2 kg/trap haul, respectively, despite an overall increase in effort from 1980 levels [Fig. 2]). Unlike the Avalon Peninsula fishery, spring catch rates in this area consistently reflect growth and recruitment into the commercial biomass as newly molted individuals recover to commercial acceptability over winter.

Research cruise CPUE and shell condition data

Logbook-derived commercial CPUEs and research cruise CPUE data with calculated confidence intervals are represented in Figures 3 and 4, respectively. Confidence intervals for most offshore Avalon research cruise CPUE data are fairly tight, with the exception of those data from a February 1986 cruise.

[4] Taylor, D. M., and P. G. O'Keefe. 1987. Analysis of the snow crab (*Chionoecetes opilio*) fishery in Newfoundland for 1986. Can. Atl. Fish. Sci. Advis. Comm. CAFSAC Res. Doc. 87/57, Dartmouth, Nova Scotia, 26 p.

These CPUE values were derived from only four fishing sets that were placed on the commercial fishing grounds opportunistically.

On the commercial fishing grounds off the Avalon Peninsula, CPUE's derived from research cruises were nearly identical to those of commercial enterprises at approximately 19.5 kg/trap haul in 1979 (spring). However, CPUEs diverged over the years primarily because commercial vessels had a greater fishing range than the research vessels. Nevertheless, the sharp drop in CPUE between 1982 and 1983 was reflected in both the commercial and research cruise data. In the commercial fishery, CPUE dropped from 13.8 kg/trap haul in the spring of 1982 to 8.0 kg/trap haul in the spring of 1983 (Fig. 3). This decline in crab abundance was mirrored in research cruise data, which indicate a decline from 9.3 kg/trap haul to 2.9 kg/trap haul over the same period (Fig. 4).

Research cruise data for this period in Bonavista Bay are not available. Logbook data, however, indicate that CPUE dropped by only 0.2 kg/trap haul (Fig. 4).

Data on shell conditions of legal-sized and prerecruit crabs from research cruises conducted off the Avalon Peninsula demonstrate that the drop in CPUE coincided with a decline in the proportion of new-shelled crabs from 52.4% to 18.6% (Fig. 5). In Bonavista Bay, the percentage of new-shelled animals dropped to 68.4% in the fall of 1983 from 97.7% in the spring of 1982. However, the proportion of new-shelled animals quickly rebounded to 97% in 1984 as opposed to 40.6% off the Avalon Peninsula during the same year.

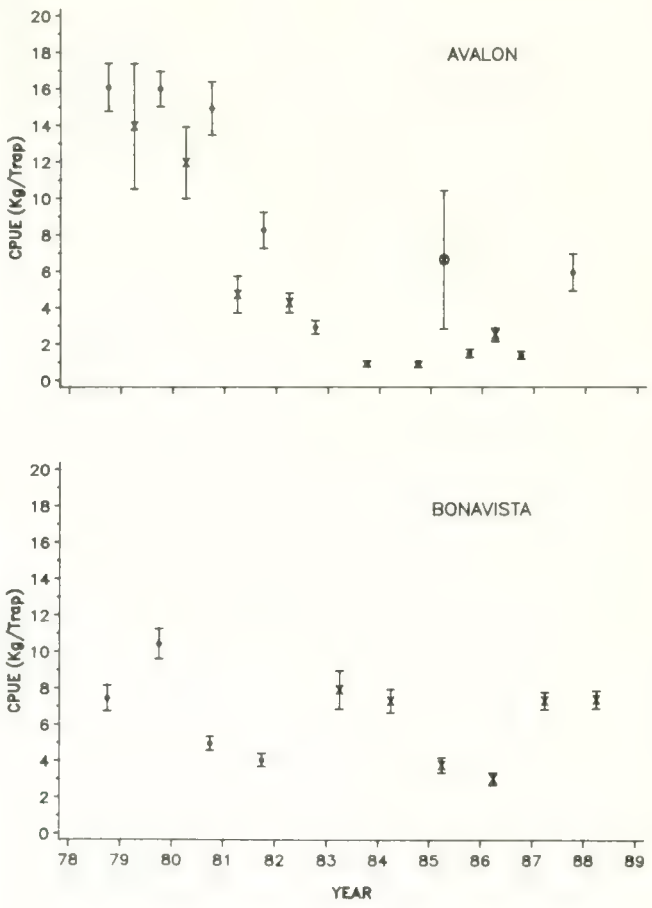

Figure 4

Research cruise CPUE's with calculated confidence intervals for the Avalon Peninsula and Bonavista Bay, 1979–88. Solid circles represent spring cruises and X's represent fall cruises. A circled 'X' is used to highlight data from the February 1986 cruise during which only 4 stations were fished in a nonrandom manner.

Temperature data

From the spring of 1978 through the first half of 1982, mean bottom temperature ranged from –0.3° C to –0.8°C off the Avalon Peninsula (Fig. 5). During the second half of 1982, the beginning of a trend towards colder bottom temperatures was evident. Bottom temperatures during this period dropped as low as –1.6 C and rarely rose above –1.0°C the entire period of mid 1982 to 1986. Two brief periods of warming occurred in both 1983 and 1984 but these periods were short-lived and weak. In 1986 a general warming trend began with an increase from the 1985 low of –1.6°C to around –1.1°C, a trend that has continued to the present.

The drop in temperature and the decrease in the proportion of new-shelled crabs appeared to coincide with bottom temperatures declining during April–May of 1982 whereas the percentage of new-shelled crabs dropped from 52.4% in April to 17.0% in September. Figure 5 illustrates that between 1982 and 1986 there were two brief periods (1983 and 1984) when mean bottom temperature at Station 27 increased slightly and coincidental increases in the proportion of new-shelled animals followed in 1984 and 1985. This delay between increase in water temperatures and appearance of new-shelled crabs is consistent with our current understanding of snow crab molting mechanisms (Moriyasu[5]).

The warming trend in July 1984 was short-lived (Fig. 5). During 1985 water temperatures dropped to the lowest level of all the years examined. Shell

[5] Moriyasu, M. Dept. Fisheries And Oceans, Gulf Fisheries Centre, Box 5030, Moncton, N.B. E1C 9B6. Personal commun. April, 1987.

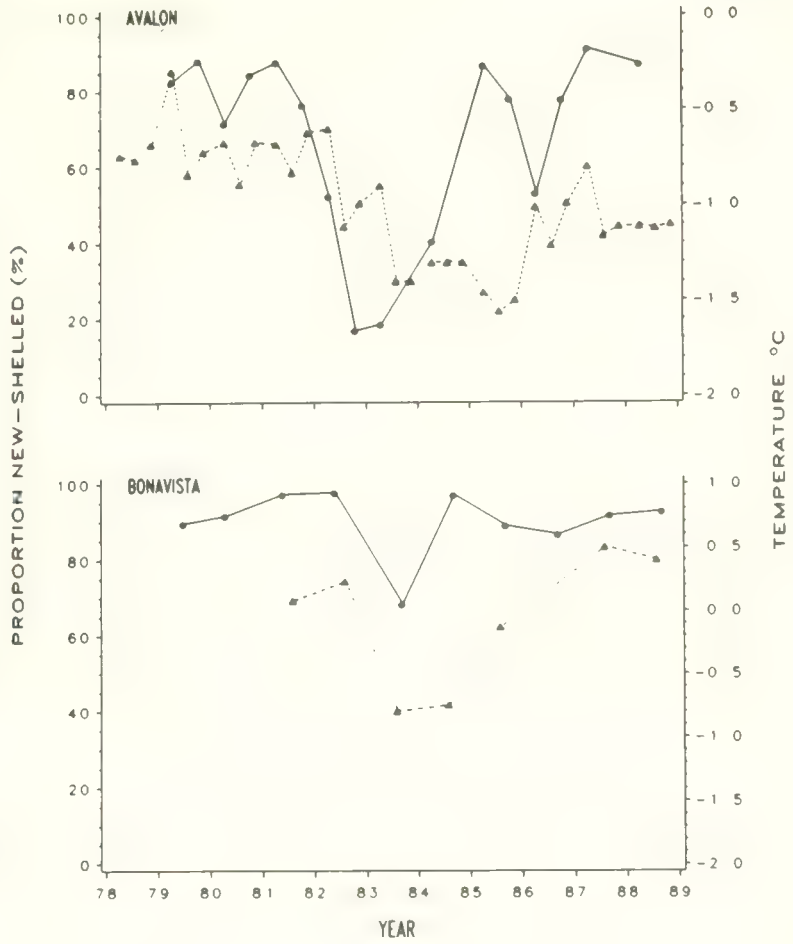

Figure 5

Changes in the percentages of new-shelled Avalon Peninsula and Bonavista Bay *Chionoecetes opilio* males ≥ 70 mm CW in relation to changes in bottom water temperatures on snow crab commercial fishing grounds, 1979–88. Solid circles connected by solid lines represent the proportion of new-shelled crabs and the triangles connected by a broken line represent bottom water temperature.

condition sampling in February 1986 indicated no molting activity during the summer and fall of 1985 (Fig. 5).

A further indication that the impact of these increases in new-shelled animals was minimal is illustrated by continuing low CPUE's (Figs. 3 and 4). Large proportions of new-shelled animals and higher CPUEs were not observed until the warming trend of 1986 was firmly established. While the decline in temperature between 1982 and 1983 is mirrored in data collected during Bonavista Bay research cruises (Fig. 5), the lowest temperatures encountered in Bonavista Bay are roughly equivalent to normal temperatures at Station 27 off Avalon Peninsula.

Although there was a significant decline in the proportion of new-shelled crab in 1983 after the water temperature declined (68.4% vs. 97.7%) in the spring of 1982 this value quickly rebounds in 1984 to 97.0% despite only a marginal warming of the water (Fig. 5).

Discussion

The tight confidence intervals for the Avalon Peninsula research cruise CPUE's (Fig. 4) for 1982–1987 (except February 1986) are indicative of just how severe, widespread, and enduring the resource depletion was in this area. Each research survey fished stations randomly selected and stratified by depth and covered virtually all the approximately 3600 sq. km. of commercial snow crab fishing grounds (Taylor et al.[6]). Had a sustained recovery been made by the crab population in any section of the commercial fishing grounds, it would have almost certainly been detected, either by our research cruises or by commercial crab fishermen.

Little is known about environmental factors that affect snow crab molting physiology. Low water temperatures may inhibit molting in crabs (Hiatt, 1948; Adelung, 1971; Leffler, 1972; Warner, 1977) and other decapods (Travis, 1954; Aiken, 1980; Ennis, 1983).

Foyle (1987) determined that snow crab from Cape Breton Island are able to maintain normal physiological functions at temperatures much higher than their normal temperature range. At high temperatures however and at temperatures below 1°C, reproductive growth and net energy consumption become slightly negative. Snow crab on the northeast coast of Newfoundland live at much lower water temperatures (<-0.75°C) than do those off the Cape Breton Island and a drop in temperature may result in such a "deficit" in their energy budget that molting physiology is impaired.

[6] Taylor, D. M., W. R. Squires, and P. G. O'Keefe. 1983. An alternate methodology for estimating snow crab (*Chionoecetes opilio*) populations in commercially fished areas. Can. Atl. Fish. Sci. Advis. Comm. CAFSAC Res. Doc. 83/1, Dartmouth, Nova Scotia, 10 p.

Aiken (1980) demonstrated that molting is inhibited in American lobsters, *Homarus americanus*, at 5° C if active premolt is not achieved before water temperature drops to that level. A similar physiological response to declining temperature may have contributed to the apparent reduction in molting in the snow crab population off the Avalon Peninsula after temperature dropped in 1982.

Molting in Newfoundland snow crab in this area generally occurs during May–August. The sharp decline in abundance of new-shelled crab in September indicated that many animals that would normally molt during this period apparently failed to do so, possibly as a result of extremely cold water temperatures.

Both Bonavista Bay and the offshore Avalon are affected by the Labrador Current. In 1982 the current became wider and deeper than in previous years causing a cooling effect throughout the water column (Akenhead[7]). Whereas this phenomenon affected the entire east coast of Newfoundland, it was most severe near the Avalon Peninsula primarily because of its comparative shallowness (174–200 m). Bonavista Bay is 220–486 m deep on the crab grounds and its depth may reduce the cooling effect of the Labrador Current (Akenhead[8]). This may explain why snow crab molting activity here was not as adversely affected as it was on the Avalon crab fishing grounds (Fig. 5).

The lack of recruitment into the fishery, between 1982 and 1986, meant that the snow crab resource off the Avalon Peninsula had been in effect "mined" rather than harvested as a renewable resource. The impact of the decline in snow crab abundance was dramatic. This marked decline in landings, from the Avalon Peninsula area, resulted in a substantial drop in employment and earnings from the snow crab fishery (Collins[9]).

Evidence of a link between temperature and molting is circumstantial. However, the drop in water temperature followed by a rapid decline in molting activity (Fig. 5), and subsequently CPUE (Fig. 4), makes a compelling argument that the yearly proportion of snow crab molting in an area is largely dependent on environmental conditions in the particular case where temperatures are very low and variable. The argument is supported by the observation that twice between 1984 and 1988 water temperatures rose and fell, affecting subsequent changes in the proportions of crabs molting off the Avalon Peninsula (Fig. 5). If molting of pre-recruit snow crabs and consequent recruitment into the fishery are affected by changes in water temperature, the impact of these changes should be included in resource management programs. The existing policy of allowing yearly exploitation rates of 50–60% should be re-examined. As the effects of these environmental changes may be long term, recommended exploitation rates could be reduced to prolong a fishery in which recruitment has been interrupted. Assessments of the fishery off the Avalon Peninsula (Taylor and O'Keefe[4]) indicate that exploitation rates were <65% between 1979 and 1981. However, owing to the failure of undersized males to molt into the fishery beginning in 1982, each successive year's standing stock was reduced until fishing was no longer economically viable. In contrast, although exploitation rates in Bonavista Bay consistently exceeded 75% (Taylor and O'Keefe[10], 1983[11], 1984b[12], and 1987[4]), molting within the population continued to provide sufficient recruitment for a viable fishery even though catch rates declined. With the exception of 1983 when the incidence of new-shelled animals (shell condition 1 and 2) in research cruise catches fell to 68% (Fig. 5), new-shelled animals composed in excess of 85% of the catch of legal-sized and immediate pre-recruits. This high level of molting appears to have prevented the precipitous decline in catches experienced in the offshore Avalon Peninsula area.

To prevent future declines of such proportions it may be advisable to monitor temperature, catch rates, and crab shell condition more closely on a seasonal basis. Efforts should also be made to determine thermal requirements for molting in snow crab. The implications for resource management strategy are simply that, regardless of exploitation levels, changes in temperature likely affect molting and hence recruitment to the standing stock to such an extent that assumptions regarding long-term sustainability of annual landings are not justified.

[7] Akenhead, S. A. 1986. The decline of summer subsurface temperatures on the Grand Bank, at 47°N, 1978–1985. NAFO SCR Doc. 86/25, 8 p.

[8] Akenhead, S. A. Institute of Ocean Sciences, Box 6000, Saanich Rd. Sydney, B.C. V8l 4B2. Personal commun., April 1987.

[9] Collins, J. F. Chief, Economic Analysis Division, Program Coordination & Economics Branch, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, Newfoundland A1C 5X1. Personal commun. September 1993.

[10] Taylor, D. M., and P. G. O'Keefe. 1981. Assessment of snow crab (*Chionoecetes opilio*) stocks in Newfoundland, 1979. Can. Atl. Fish. Sci. Advis. Comm. CAFSAC Res. Doc. 81/57, Dartmouth, Nova Scotia, 34 p.

[11] Taylor, D. M., and P. G. O'Keefe. 1983. Assessment of snow crab (*Chionoecetes opilio*) stocks, in Newfoundland in 1980. Can. Atl. Fish. Sci. Advis. Comm. CAFSAC Res. Doc. 83/3, Dartmouth, Nova Scotia, 40 p.

[12] Taylor, D. M., and P. G. O'Keefe. 1984b. Assessment of Newfoundland snow crab (*Chionoecetes opilio*) stocks in Newfoundland for 1982. Can. Atl. Fish. Sci. Advis. Comm. CAFSAC Res. Doc. 84/3, Dartmouth, Nova Scotia, 30 p.

Acknowledgments

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Literature cited

Adelung, D.
1971. Studies on the molting physiology of decapod crustaceans as exemplified by the shore crab (*Carcinus maenas*). Sci. Mar. Res. at Heligloland 22:66–119. (English translation by Fish. Res. Board Can., Transl. Ser. No. 1877.)

Aiken, D. E.
1980. Molting and growth, Chapter 2. *In* J. S. Cobb and B. F. Phillips (eds.), The biology and management of lobsters, Vol. 1: Physiology and behavior. Academic Press, 463 p.

Ennis, G. P.
1983. Variation in annual growth in two Newfoundland lobster (*Homarus americanus*) populations in relation to temperature conditions. ICES C.M.1983/K:24, 11 p.

Foyle, T. P.
1987. Metabolism and energetics in a cold-water crustacean: the snow crab, *Chionoecetes opilio*. M.Sc. thesis, Dalhousie Univ., 83 p.

Hiatt, R. W.
1948. The biology of the lined shore crab, *Pachygrapsus crassipes* Randall. Pacific Sci. 2:135–218.

Leffler, C. W.
1972. Some effects of temperature on the growth and metabolic rate of juvenile blue crabs, *Callinecetes sapidus*, in the laboratory. Mar. Biol. 4:104–110.

Miller, R. J., and P. G. O'Keefe.
1981. Seasonal and depth distribution, size, and molt cycle of the spider crabs, *Chionoecetes opilio*, *Hyas araneus*, and *Hyas coarctatus* in a Newfoundland bay. Can. Tech. Rep. Fish. Aquat. Sci. 1003:iv + 18 p.

Paul, A. J.
1984. Mating frequency and viability of stored sperm in the tanner crab *Chionoecetes bairdi* (Decapoda, Majidae). J. Crust. Biol. 4(3):375–381.

Taylor, D. M., G. W. Marshall, and P. G. O'Keefe.
1989. Shell hardening in snow crabs *Chionoecetes opilio* tagged in soft-shelled condition. N. Am. J. Fish. Manage. 9:504–508.

Travis, D. F.
1954. The molting cycle of the spiny lobster, *Panulirus argus* Latreille. I: Molting and growth in laboratory-maintained individuals. Biol. Bull. 107:433–450.

Warner, G. F.
1977. The biology of crabs. Van Nostrand Reinhold Company, New York, 202 p.

Spawning time and recruitment dynamics of larval Atlantic menhaden, *Brevoortia tyrannus*, into a North Carolina estuary

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Abstract.—Larval Atlantic menhaden, *Brevoortia tyrannus*, were collected weekly during their expected recruitment (November–April) to the estuary near Beaufort, North Carolina, over seven consecutive years beginning 1985–86. The larval density in nighttime quantitative samples was calculated and ages determined from otolith microstructure. Back-calculated birthdates and larval abundance data were used to estimate the relative contribution of weekly age cohorts to seasonal recruitment of larvae. Summaries of these data were measures of the spawning distributions. Larvae were recruited to the estuary from mid-November through April, with about 86% collected during February–April. In all years, age and size of larvae increased linearly throughout recruitment until the end of March and then declined. The mean age of recruited larvae over all years was 61 days and the mean standard length was 24.6 mm. Atlantic menhaden spawning season was protracted, lasting 4–6 months. In every spawning season, a dominant birthweek mode in either December or January contributed from 25–43% of the total recruits. More than 76% of all spawning occurred in the December– January period. Individual birthweek cohorts recruited to the estuary over periods from one week to several months. Cohorts that usually contributed the greatest number of individuals to estuarine recruitment usually recruited over longer periods. Atlantic menhaden have apparently selected a spawning season and location that ensures transport of larvae across the southeast United States continental shelf and arrival of most larvae during a time when conditions are conducive to optimal survival in the estuary.

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The Atlantic menhaden, *Brevoortia tyrannus*, is a commercially important clupeid that ranges on the east coast of the United States from the Gulf of Maine to the central coast of Florida. Tagging studies have shown that this species makes extensive seasonal migrations northward along the coast in spring and southward in fall and winter (Dryfoos et al., 1973; Nicholson, 1978). Most of the population is thought to overwinter in the area between Cape Hatteras, North Carolina, and northern Florida (Ahrenholz et al., 1987). Spatial and temporal trends in Atlantic menhaden spawning have been suggested by studies on the distribution of eggs and larvae (Reintjes, 1961; Kendall and Reintjes, 1975; Judy and Lewis, 1983) and studies on ovarian maturity and fecundity (Higham and Nicholson, 1964; Lewis et al., 1987). Those studies show that spawning occurs off New England from late spring to early summer and again in early fall, off the mid-Atlantic states in spring and fall and off the southeastern states from October to March. Maximum numbers of menhaden probably spawn in winter in offshore waters south of Cape Hatteras (Reintjes, 1969; Judy and Lewis, 1983) and waters off the North Carolina coast may be one of the major spawning grounds for Atlantic menhaden (Higham and Nicholson, 1964).

Plankton collections taken off North and South Carolina suggest that Atlantic menhaden may continuously spawn from late fall to early spring. Collections taken in the vicinity of Beaufort, North Carolina, from 1955 to 1961 (unpubl. data, National Marine Fisheries Service, Beaufort Laboratory, cited by Higham and Nicholson, 1964) showed larvae in samples beginning in November or early December and continuously thereafter until mid-April. Subsequent work supported these estimates of the timing of estuarine immigration of menhaden larvae. Lewis and Mann (1971) sampled larval menhaden semimonthly as the fish recruited to the estuary near Beaufort Inlet in the fall/winter 1966–67 and 1967–68 seasons, to estimate relative indexes of abundance. Densities of menhaden larvae recruited to estuaries were reported for North Carolina (Hettler and Chester, 1990; Warlen and Burke, 1990) and South Carolina (Allen and Barker, 1990).

Examination of otolith microstructure to count daily growth increments has made possible reasonably accurate estimates of the age and growth of the early life history stages of fishes. Age at estuarine recruitment can be tracked within and among seasons or years. Age at

recruitment is also a measure of the total time from offshore spawning to recruitment to the estuary. Valuable new information on the early life history of larvae can be obtained when estimates of recruitment densities are combined with estimates of seasonal age composition of the catches. Back-calculated birthdate distributions of larvae in each sample can be multiplied by the catch density to determine the relative contribution of birthweek cohorts to the number of immigrants.

The purposes of this seven-year study were to document the duration and relative abundance of larval Atlantic menhaden recruitment to the estuary near Beaufort, North Carolina; to measure size and estimate ages of recruited larvae; to back-calculate birthdate distributions of larvae; and to determine the contribution of birthweek cohorts to the number of immigrants for an estimation of temporal spawning within and among sampling years.

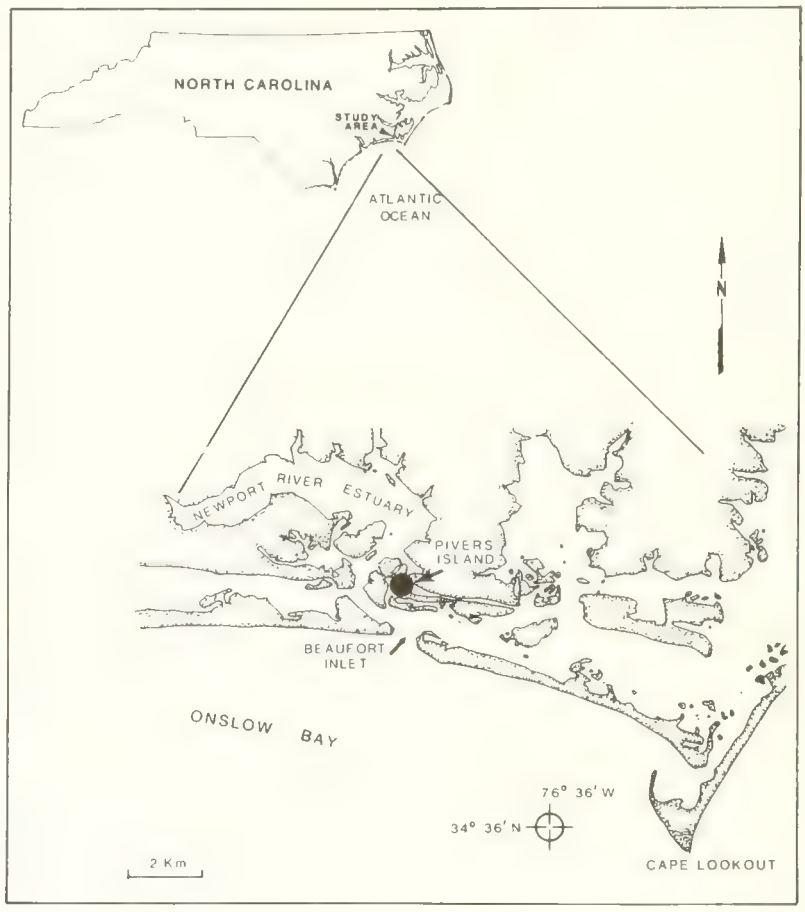

Figure 1

Location of the sampling site for larval Atlantic menhaden, *Brevoortia tyrannus*, in the lower Newport River estuary near Pivers Island, North Carolina.

Methods

Larval collection

Larval Atlantic menhaden were collected at a station adjacent to Pivers Island (Fig. 1) as they recruited to the Newport River estuary from the Atlantic Ocean. Sampling, designed to cover the expected recruitment period of mid-November to April (Lewis and Mann, 1971), ran for seven consecutive years beginning with the 1985–86 sampling year. Larvae were sampled from 13 November 1985 to 23 April 1986 with a 60-cm bongo frame with paired 505-µm mesh nets and flow meters pulled by a 6.7-m boat. Tows were made weekly during nighttime hours just after mid-flood tide, when the current was strongest, to reduce potential net avoidance by larvae. Data from the catch of both nets from two consecutive tows, one surface-bottom-surface (double oblique) in 3–5 m of water and one just under the surface (subsurface), were averaged to estimate larval density (number larvae/100 m^3 water fished) and to provide fish for ageing. The lack of a significant difference (paired comparison t-test, $P>0.05$) in catch density from subsurface and double oblique tows allowed the paired data to be combined. In the other six sampling years (19 November 1986–30 April 1987, 10 November 1987–4 May 1988, 16 November 1988–3 May 1989, 15 November 1989–2 May 1990, 14 November 1990–24 April 1991, and 13 November 1991–6 May 1992) larvae were collected, with a 1 × 2 m neuston net frame fitted with a 945-µm mesh net and flow meter fished just under the water surface from a bridge platform over the center of the channel adjacent to Pivers Island. This location was only meters from the site sampled with the bongo nets in 1985–86. As in 1985–86, all samples were collected weekly during nighttime hours at mid-flood tide. Three consecutive sets were made each night in 1986–87 and four each night in subsequent years. Because of the expected seasonal variation in menhaden abundance, sets were between 2 and 16 minutes long; most were 5–7 minutes long. Volume of

water fished by the net ranged from 41 to 805 m^3 but most sets filtered 150–350 m^3. Ichthyoplankton samples were preserved with 95% ethanol and diluted so that the final alcohol concentration was ≥70%. Samples not sorted within 24 hours were rinsed and represerved in 70% ethanol. As for bongo nets, these catches were standardized as the number of Atlantic menhaden/100 m^3 of water fished. The mean of the density data from all sets on a given night (bongo nets in 1985–86 and neuston nets in other years) was used as the estimate of density of Atlantic menhaden larvae recruited during the flood tide.

Simultaneous larval collections were made with bongo and neuston nets on 17 December 1986 (3 sets) and 18 March 1987 (4 sets) to test for differences in menhaden catch density between gear type. There were no significant differences in density of menhaden caught by gear type (ANOVA, $P>0.54$) or among sets (ANOVA, $P>0.24$). Hence, the catch data from bongo and neuston nets are comparable. The mean age or standard length (SL) also did not differ between the two types of nets.

Larval ageing

Larvae for ageing were subsampled from individual weekly night net sets in proportion to their contribution to the total nightly catch. In catches of up to 20 fish, all larvae were used. In catches of >20 fish, subsample sizes were proportional to catch but generally no more than 50 fish were aged per week. The ages of 3,864 larvae were determined.

The standard length of each larva to be aged was measured to the nearest 0.1 mm with an ocular micrometer. Sagittal otoliths were removed from their surrounding soft tissue, cleaned in distilled water, and placed on a glass microscope slide under a thin layer of Flo-Texx mounting medium. Otoliths were observed with transmitted light on a compound microscope fitted with a television camera. Growth increments were counted from images on a video monitor at microscope magnifications of 400× or 1,000×. One person made dual readings of otoliths from each fish. Readings were averaged if they differed by a count of four or less; if they differed by ≥5 increments, the fish was excluded from further analyses. Increment counts of about 2% of the aged fish differed by five or more. Estimated age was the number of increments counted plus an empirically derived value for the number of days (5) from spawning to first increment formation (Warlen, 1992). The otolith ageing technique for Atlantic menhaden larvae has been validated by Maillet and Checkley (1990), who established that larvae form one otolith growth increment per day. I assumed that the age at initial increment deposition did not vary and that the otolith increment deposition rate was constant within and between sampling seasons. A spawning date (birthdate) was assigned to each ageable larva by using the estimated age of the fish in days to back-calculate from the date of capture. Larvae spawned in a given calendar week were considered in the same calendar birthweek cohort.

Estuarine recruitment of birthweek cohorts

The percentage contribution of Atlantic menhaden larvae of all birthweek cohorts to the total recruitment was measured for each of the seven years from 1985–86 to 1991–92. For each weekly collection, the percentage of larvae spawned in each back- calculated birthweek was determined. Each percentage was then multiplied by the total larval density (number/100 m^3) for the week. Based on these results, density estimates were made for larvae from each birthweek cohort recruiting to the estuary on a given collection night.

Densities for each birthweek cohort were summed over all collections within a sampling year. The proportion that each birthweek cohort contributed was determined by dividing the individual birthweek sums by the total density of all birthweek cohorts for the recruitment year. These computations produced estimates of the relative contribution that each birthweek cohort made to the total recruitment of menhaden larvae into the estuary near Beaufort.

Results

Larval recruitment abundances

Larval Atlantic menhaden recruited to the estuary near Beaufort over a 5 to $5^1/_2$ month period from mid-November to the end of April (Fig. 2). Larvae were generally recruited in highest densities during February–April and contained, on average, about 86% of the total estuarine recruitment during those months (Table 1). Recruitment was low in November and seldom extended into May. There was a distinct density mode in each of the seven years (Fig. 2). Except for 1988–89, modal density always occurred in March or April (Fig. 2, Table 2). Highest densities in a 3-week period (modal week plus adjoining weeks) in any year contributed 32–89% of the total density of Atlantic menhaden larvae for the year (Table 2).

During the recruitment period, most Atlantic menhaden larvae recruited to the estuary in pulses. Mean density varied from zero to about 570 larvae/100 m^3 and most samples contained <20 larvae/100 m^3 (Figs. 2 and 3). Catch densities varied among sets on any given night and the standard deviation in catch densities generally increased with the mean catch den-

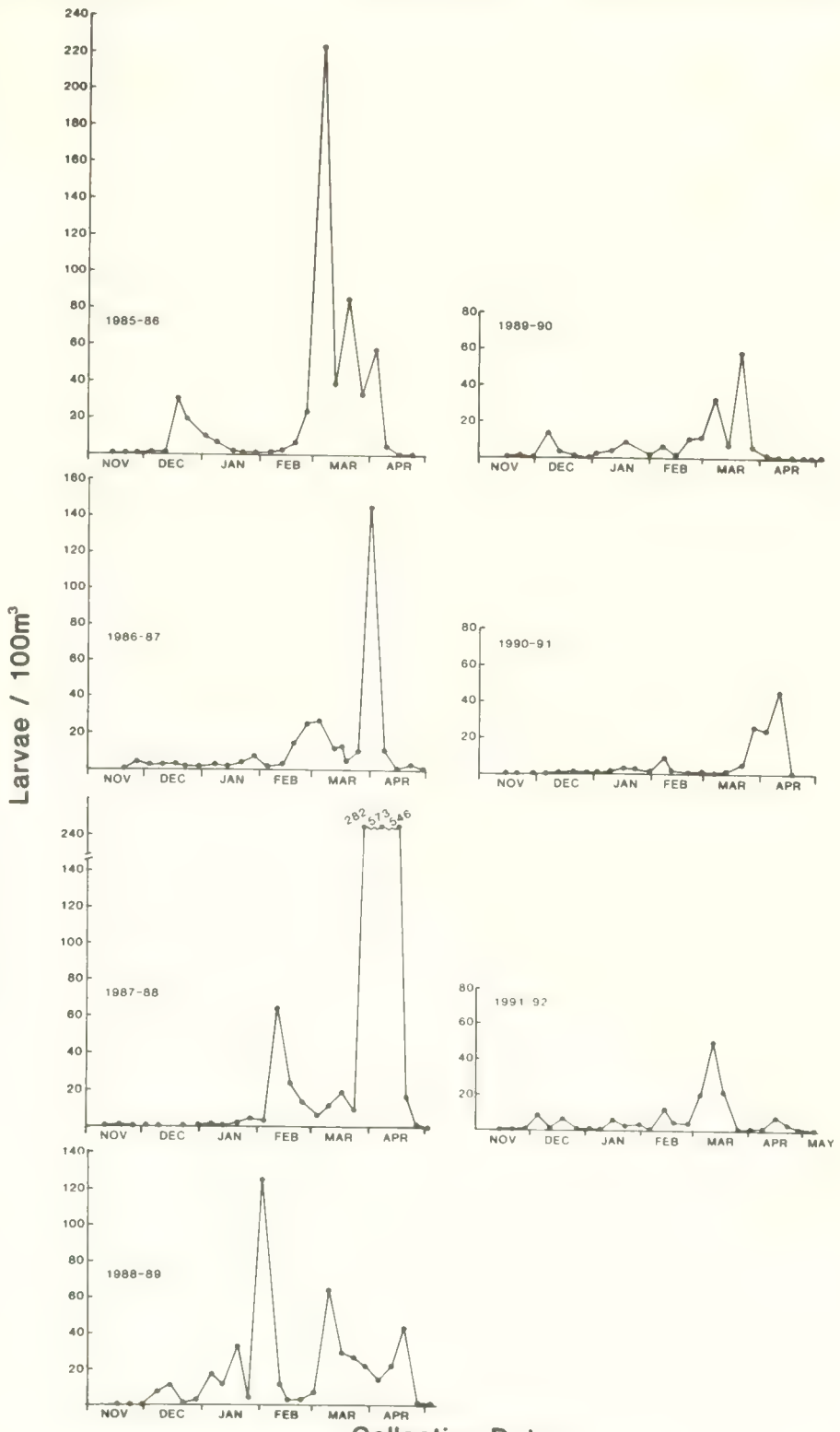

Figure 2

Weekly mean density (larvae/100 m^3) of Atlantic menhaden, *Brevoortia tyrannus*, larvae in collections at Pivers Island, North Carolina, in the lower Newport River estuary during seven consecutive estuarine recruitment years.

sity (Fig. 3). Relative abundance of larvae also varied among years (Fig. 2). The sum of weekly densities for individual sampling years differed by more than an order of magnitude (Table 2). Lowest relative abundances were observed for the last three sampling years.

I assumed that larval Atlantic menhaden caught each week were newly recruited to the estuary and that they were in transit past Pivers Island to upper portions of the estuary. These assumptions are supported by the presence of an abundance mode on 19 December 1985 (Fig. 2) and the presence of similar modes from bongo net sampling in the same estuary one-week later about 6 km up-estuary and two-weeks later about 11 km up-estuary (Warlen, unpubl. data). Also, the generally narrow 95% confidence limits in the age of larvae within each collection, along with no increase in the confidence limits through the recruitment year (Fig. 4), does not suggest an increase in the number of different birthweek cohorts in the lower estuary. In a number of cases, the week following a peak in density showed relatively low recruitment (Fig. 2), a pattern that did not suggest substantial carryover and accumulation of larvae from week to week. While a single sampling location may not reflect patterns of larval estuarine recruitment for all areas south of Cape Hatteras, it does provide a time-series description of relative larval recruitment abundances over several years inside a large inlet near the presumed major fall/winter spawning area.

Age and size of larvae

In every sampling year the age of larvae increased linearly throughout estuarine recruitment until about the end of March after which the mean age declined (Fig. 4). Linear regressions of the mean estimated age over time, excluding the end-of-season down trending values, were significant (ANOVA, $P<0.001$) for each recruitment year. Young larvae were always collected early in each recruitment year (Fig. 4). Virtually all larvae collected in November were less than 40 days old. Larvae collected about late March were 2–4 times older than larvae collected early in the recruitment year. Except in a few cases, the within-sample age variation was small and the 95% confidence limits were within ±5 days of the mean age.

Larvae recruited to the estuary during peak recruitment were also the older larvae. Peak recruitment densities were in February–April (Fig. 2) and those larvae were older, generally age 60–90 days or older, as in 1987–88 when some were up to age 115 days (Fig. 4). The recruitment-year mean age of larvae varied between 55 and 74 days for the seven years. The mean age of larvae over all years was 61 days.

The standard length of larvae also increased significantly (ANOVA, $P<0.001$) within each recruitment year. The mean size of larvae increased to the end of March then decreased slightly to

Table 1

Percentage of the sum of the weekly mean densities (number/100 m^3) of larval Atlantic menhaden, *Brevoortia tyrannus*, recruited to the estuary near Pivers Island, North Carolina, November–May of each recruitment year.

Recruitment year	Month						
	Nov	Dec	Jan	Feb	Mar	Apr	May
1985–86	0.0	9.4	3.9	6.3	68.8	11.6	0.0
1986–87	1.6	4.1	5.5	15.1	18.5	55.2	0.0
1987–88	<0.1	<0.1	0.5	6.7	20.8	71.9	<0.1
1988–89	<0.1	5.0	14.4	30.9	32.2	17.4	<0.1
1989–90	1.2	10.7	12.8	16.9	57.0	1.4	0.0
1990–91	0.0	2.1	7.3	10.0	26.1	54.5	0.0
1991–92	0.5	10.4	8.5	13.5	57.5	9.5	0.1
Mean	0.5	6.0	7.6	14.2	40.1	31.6	<0.1

Table 2

Sum of weekly mean densities (number/100 m^3) by year, relative abundance (related to 1990–91), and peak recruitment density period (highest three consecutive sampling-date catches including the mode) of larval Atlantic menhaden, *Brevoortia tyrannus*, collected at Pivers Island, North Carolina, by recruitment year.

Recruitment year	Sum of weekly mean densities	Relative abundance	Peak recruitment density			
			Period of highest three consecutive catches			% of year
1985–86	554	4.3	Mar	5–Mar	19	59.9
1986–87	288	2.3	Mar	25–Apr	8	57.7
1987–88	1581	12.4	Mar	30–Apr	13	88.6
1988–89	459	3.6	Jan	19–Feb	1	32.2
1989–90	173	1.4	Mar	7–Mar	21	53.4
1990–91	128	1.0	Mar	27–Apr	10	75.2
1991–92	163	1.3	Mar	4–Mar	17	56.7

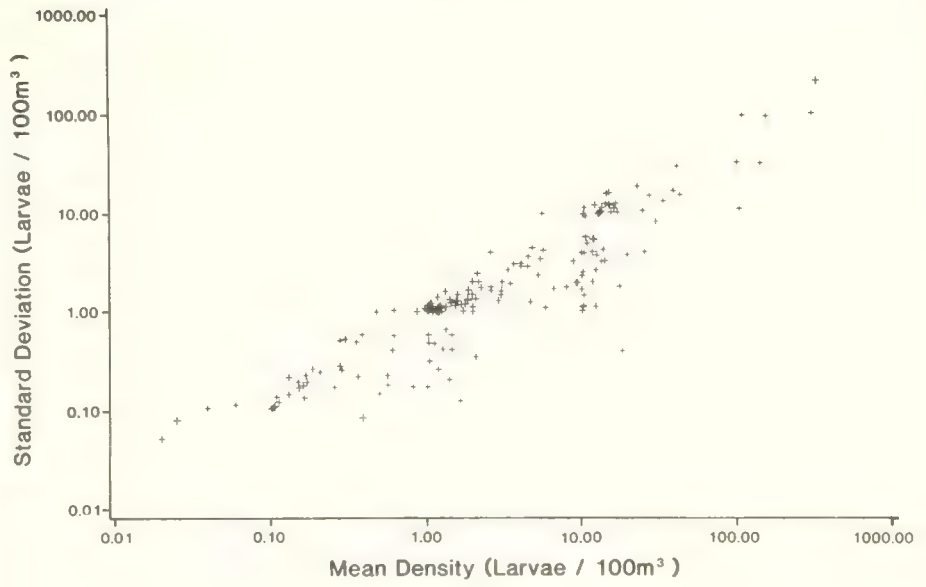

Figure 3

Plot of standard deviation versus mean density (larvae/100 m^3) for each collection night for larval Atlantic menhaden, *Brevoortia tyrannus,* sampled at Pivers Island, North Carolina, for seven consecutive recruitment years.

the end of the recruitment year (Fig. 5). Larvae recruited to the estuary were always >20 mm SL, except early in the recruitment year (November–December) when the mean size could be as low as 15 mm (Fig. 5). The overall recruitment year mean SL of larvae varied between 23.2 and 25.4 mm for the seven years and the mean SL over all years was 24.6 mm.

Spawning time

The menhaden spawning season in North Carolina was estimated from the birthdate distributions of larvae that survived to recruit to the estuary. The percentage distribution of spawning by week (Fig. 6) was based on the relative abundance of larvae collected at Pivers Island throughout the recruitment year. The spawning season was protracted, lasting four to six months (Fig. 6). Estimated spawning was variable among birthweeks. In every spawning season, there was a dominant birthweek mode that contributed from 25 to 43% of the total estuarine recruits. Except for 1987–88 (20 December 1987), these modes occurred very close to the new moon phase of the lunar cycle (10 January 1986, 31 December 1986, 9 December 1988, 28 December 1989, 15 January 1991, and 6 December 1991). Median spawning and modal spawning peaks were always in December or January as were the second and third quartile intervals of the distributions, except in 1989–90 when the second quartile interval extended into November (Fig. 6). Over all seven years, an average of more than 76% of all spawning occurred in December–January (Table 3). Earlier season spawning (October–November) contributed an average of 16% of the total, although November spawning alone could sometimes account for about 26% (Table 3). Little spawning occurred in February (. 7%) and in only two years did the March contribution exceed 1%.

The data suggest that within-season spawning frequency may be multimodal. There was an indication in 1985–86, 1986–87, 1989–90, 1990–91, and 1991–92 that a small, early mode may have occurred in October or November (Fig. 6). If there was an early mode in 1988– 89, it may have blended with the mode for later spawned fish. A small, late season mode (February or March) may also have been present and was most evident in the 1986–87, 1988–89, 1989–90, and 1991–92 spawning seasons.

Recruitment of birthweek cohorts

Individual birthweek cohorts were recruited to the estuary over periods from one week to several months (Fig. 7). Those birthweek cohorts that recruited over the shortest time periods were generally spawned either early (October) or late (February–March) in the season. Birthweek cohorts spawned from mid-November through January usually recruited over

Table 3

Percentage monthly spawning of Atlantic menhaden, *Brevoortia tyrannus*, estimated from the density-weighted, back-calculated birthdate distributions of larvae recruited to the estuary near Pivers Island, North Carolina, during November–April each recruitment year.

Recruitment year	Spawning month					
	Oct	Nov	Dec	Jan	Feb	Mar
1985–86	0.4	12.8	17.3	68.3	1.2	0.0
1986–87	4.2	7.3	64.4	21.1	2.9	0.1
1987–88	0.1	5.9	63.4	30.5	0.1	0.0
1988–89	0.6	26.5	49.2	9.1	12.9	1.7
1989–90	6.6	22.4	31.9	36.4	2.5	0.2
1990–91	0.0	8.4	11.6	54.2	25.8	0.0
1991–92	7.6	9.2	62.3	16.5	2.1	2.3
Mean	2.8	13.2	42.9	33.7	6.8	0.6

the longest time periods. However, 70% or more of any cohort were usually recruited in ≤3 consecutive weeks. In each recruitment year, those birthweek cohorts with the greatest numbers of individuals contributed most to the estuarine recruitment mode (Fig. 7). Also, within the larval catch of any given week, from one to 10 birthweek cohorts were represented (Fig. 7).

Discussion

Relatively large schools of larger-sized Atlantic menhaden, migrating from New England and mid-Atlantic states, along with local (North Carolina at least) Atlantic menhaden emigrating from estuaries, spawn off the southeast Atlantic states. The area from Cape Hatteras to about northern Florida is thought to be the major spawning location for this species (Higham and Nicholson, 1964; Reintjes, 1969; Nelson et al., 1977; Judy and Lewis, 1983; Lewis et al., 1987). Although the previous studies suggested that Atlantic menhaden spawn in the fall and winter off the southeast Atlantic states, none were able to estimate within season spawning intensity. The present study, which utilized samples collected throughout the recruitment year, estimated within season spawning intensity based on survivors entering an estuary. However, without any knowledge of egg production and the survival of cohorts between offshore spawning and estuarine recruitment, it was not possible to know how closely the estimates of the birthdate distributions represented the actual seasonal egg production.

In each year, the Atlantic menhaden spawning season was protracted. This long spawning season might indicate a "bet hedging" strategy (Lambert and Ware, 1984) where eggs are released continuously over the spawning season to ensure some reproduction during the most favorable periods for survival. Based on the birthdate distributions of larvae that recruit to the estuary, the most favorable period each year appears to be for those fish spawned in a relatively short period between early December and mid-to-late January. For all seven years, it was within this major spawning period that the week of peak spawning occurred. Larvae from this major spawning period are probably progeny of the large menhaden schools migrating southward from the New England and mid-Atlantic states. These schools, which contain many fish of spawning age (3+ years), are harvested from about late November to late January during the North Carolina fall purse seine fishery (Smith et al., 1987). Larvae spawned earlier (October–November), may originate from adults inhabiting North Carolina coastal waters and estuaries in the summer or from early fall adult immigrants to North Carolina waters (Wilkens and Lewis, 1971). Larvae spawned late (February–March) may have been spawned further south and immigrated to the estuary late in the season or were the offspring from northward migrating adults in early spring. This late spawned group contributed the younger, smaller larvae observed at the end of the recruitment year (Figs. 4 and 5).

Spawning locations, and routes and rates of transport probably account for the variation in age of larvae recruited to the estuary. While the precise locations of menhaden spawning are not known, the general area is thought to be on the mid- to outer-continental shelf off North Carolina (Checkley et al., 1988; Warlen, 1992). However, accounts of the occurrence of eggs are limited (Reintjes, 1969; Judy and Lewis, 1983) and no records of actual spawning events exist. Although some early season spawning may occur closer to shore, the largest contribution of recruited larvae to the estuary is later in the season, probably from the warm, plankton rich areas closer to the Gulf Stream. Water temperatures are generally ≥18°C (Govoni, 1993), even in winter. These warm temperatures are due, in part, to intrusions of warm surface water onto the middle continental shelf (Atkinson, 1985). Frequent upwelling events (Pietrafesa et al., 1985) stimulate primary productivity by providing nutrients (Atkinson, 1985; Yoder, 1985) for phytoplankton growth (Yoder et al., 1983)

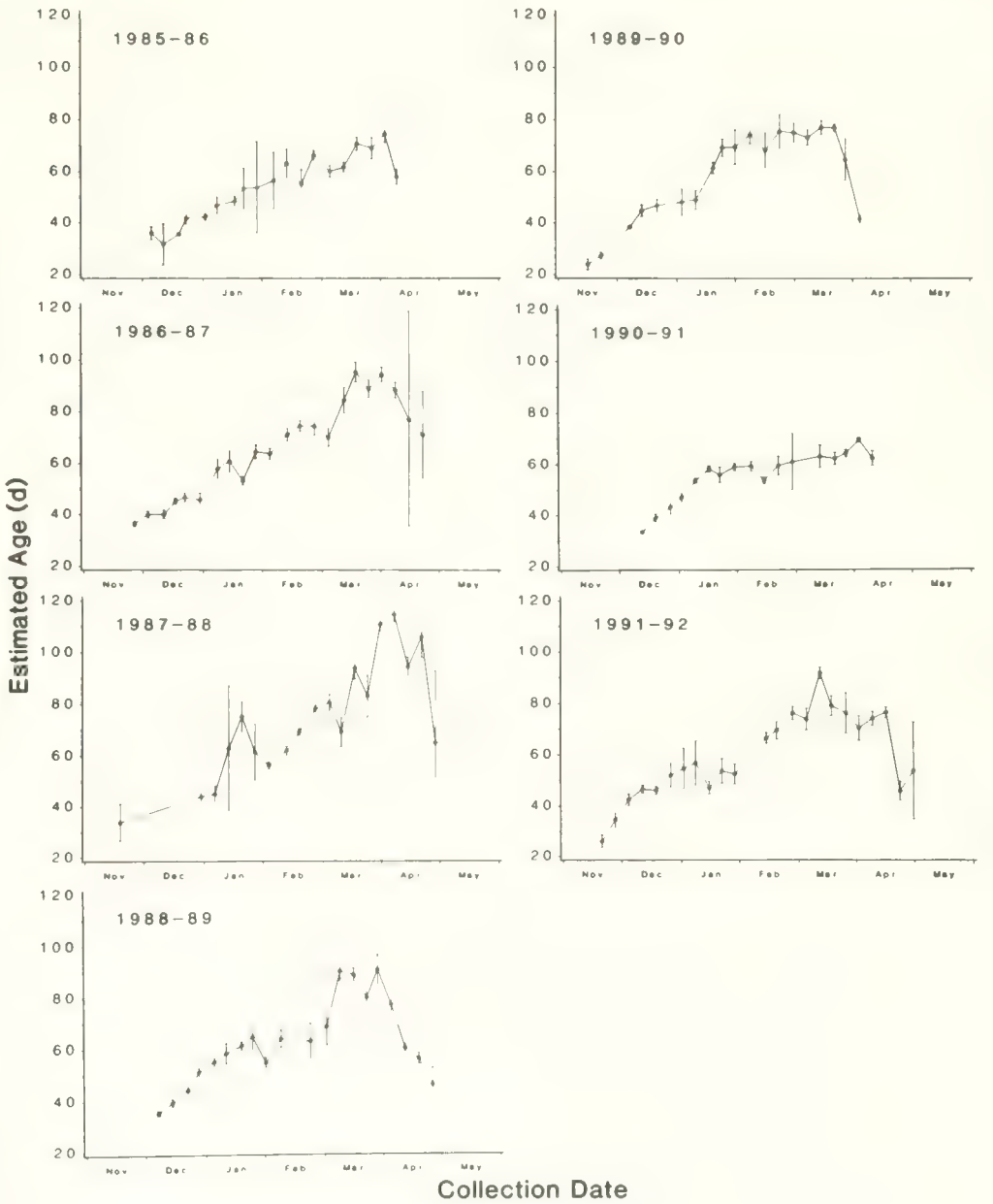

Figure 4

Mean of estimated ages (days) with 95% confidence limits of larval Atlantic menhaden, *Brevoortia tyrannus,* collected weekly over seven years during their estuarine recruitment at Pivers Island, North Carolina.

thus increasing secondary production (Paffenhöfer, 1985). This productive area is probably utilized by larval fishes spawned nearby.

Atlantic menhaden appear to spawn during periods (daily, seasonal) of lower light intensity. They probably spawn at night, and may have a diel pattern of ovulation and spawning that may be linked to the daily cycle of light and darkness as noted for many marine fishes (Bye, 1990). Reintjes (1969) examined Atlantic menhaden eggs at sea and concluded that estimated ages of groups of eggs of different stages suggested that "spawning occurred after mid-

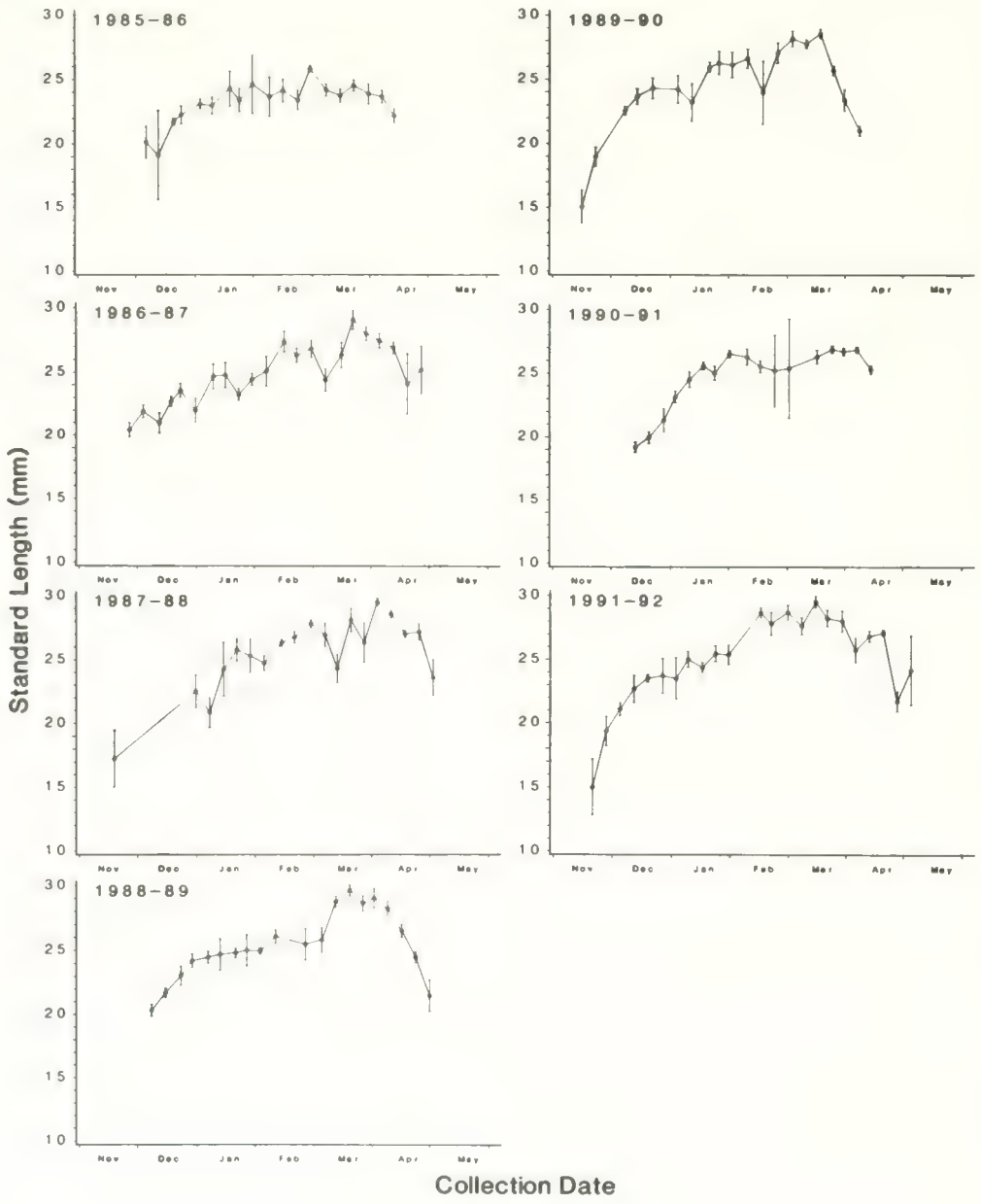

Figure 5

Mean standard length (mm) with 95% confidence limits of larval Atlantic menhaden, *Brevoortia tyrannus*, collected weekly over seven years during their estuarine recruitment at Pivers Island, North Carolina.

night but before dawn on three consecutive days." Ferraro (1981) also noted that Atlantic menhaden spawned at night and suggested that night spawning might be a means of reducing predation on spawners and eggs or of avoiding the deleterious effects of ultraviolet irradiation during early embryogenesis.

The relatively constant year-to-year spawning mode during December–January, observed in this study, occurs when the daily hours of darkness are maximal, 13 1/2–14 hours between sunset and sunrise, and when overcast days are more frequent. Peak spawning in each year (except 1987–88) also occurs very

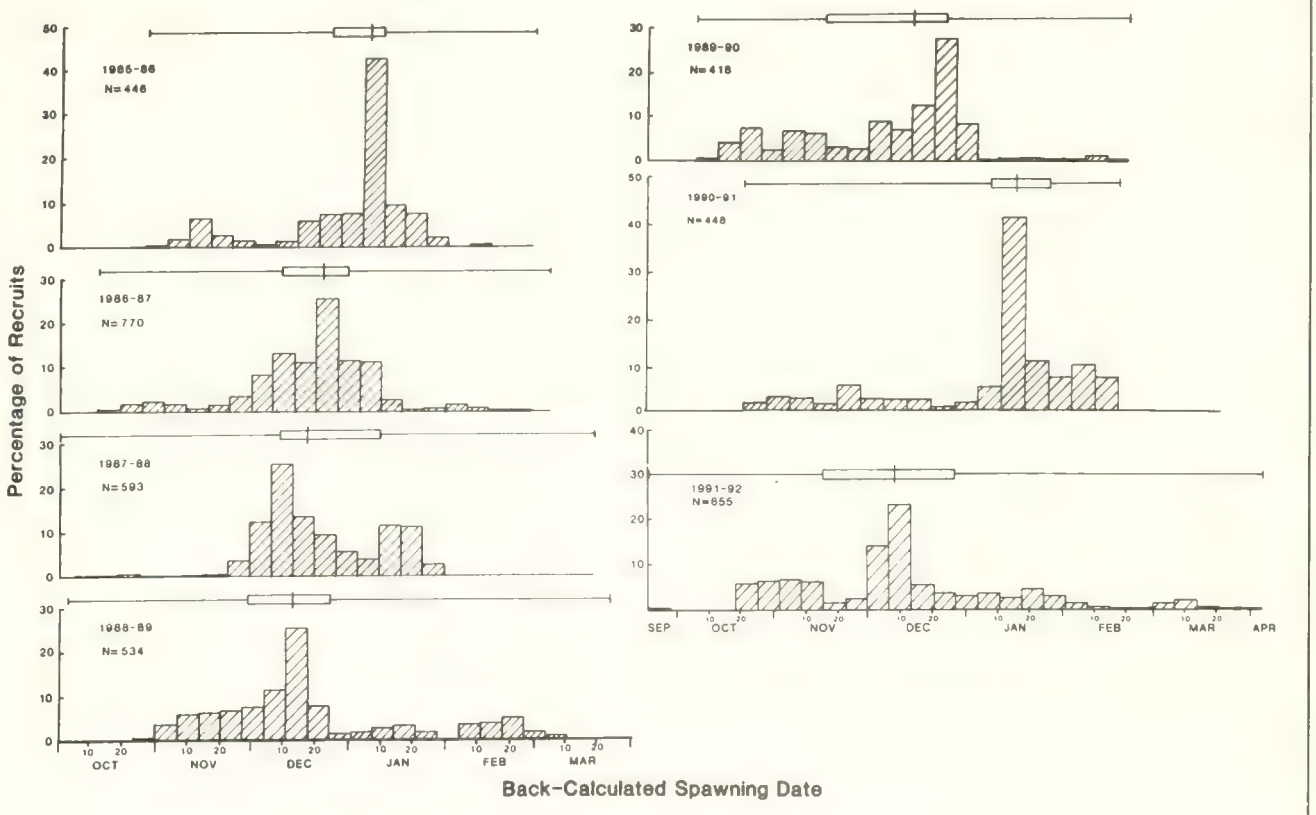

Figure 6

Birthdate frequency distributions calculated from the relative abundances of larval Atlantic menhaden, *Brevoortia tyrannus*, collected in the lower estuary at Pivers Island, North Carolina, in each of seven recruitment years. In each distribution, the vertical line is the median value and the box represents the 2nd and 3rd quartile intervals (central 50%). Lines beyond the boxes represent the range of data.

close to the new moon phase of the lunar cycle, which would also reduce available light during spawning.

Spawning of Atlantic menhaden off the southeastern Atlantic states is apparently timed to ensure transport of larvae across the continental shelf and arrival of most of the larvae (about 85% on average) during a time of optimal survival conditions in the estuary. Atlantic menhaden larvae that recruit to the estuary during the peak period (February–April) arrive when the water temperature is rising, prey abundance is high, and predator abundance and estuarine resident larval fishes and invertebrate (ctenophore) competitor abundances are low (Warlen and Burke, 1990). Some Atlantic menhaden larvae (about 15%) recruited to the estuary early in the season, November–December, before the period of coldest water temperatures in January (Warlen and Burke, 1990). These early recruited larvae may experience cold-related mortality if estuarine water temperatures drop to <4°C (Lewis, 1966; Wilkens and Lewis, 1971). However, larval Atlantic menhaden may tolerate lower temperatures than larvae of other species (e.g. spot, *Leiostomus xanthurus*) that recruit over the same period in the Beaufort area (Hoss et al., 1988). In milder winters, earlier recruited larvae may survive overwinter and, in the following spring and summer, may be larger than the more abundant Atlantic menhaden larval groups recruited several months later. Ahrenholz et al. (1989) observed a multi-modal distribution in lengths of juvenile menhaden collected in the summer in North Carolina which may reflect several seasonal abundance groups of immigrating larvae (early, middle, late) from a single spawning season.

Variation in egg production, mortality of eggs and larvae, and losses of larvae by advection to other areas of the coast probably account for the observed differences in relative recruitment abundances at the Pivers Island collection site. There was more than an order of magnitude difference between the relative abundances of the most abundant and the least abundant years. Lewis and Mann (1971) also ob-

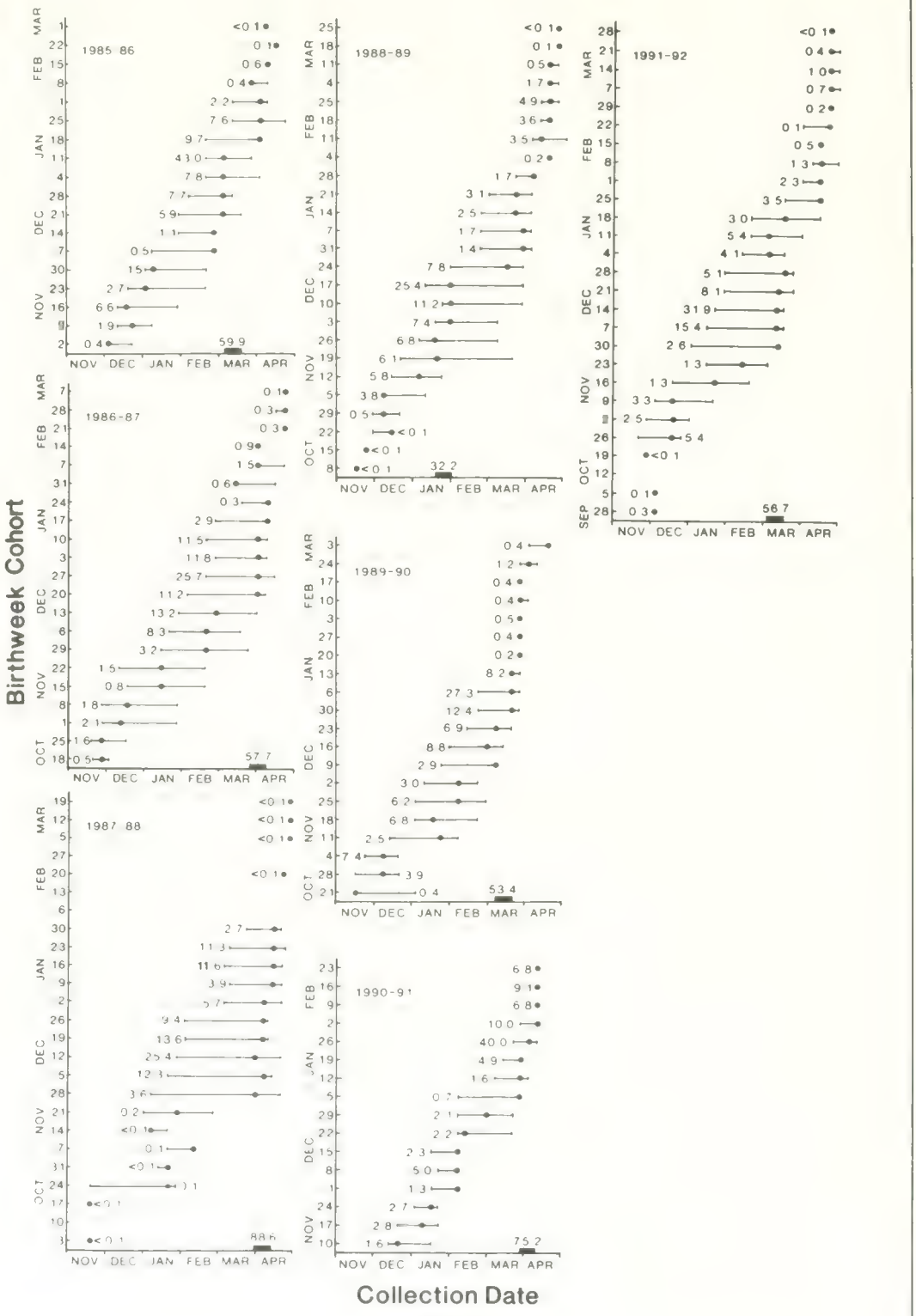

Figure 7

Percentage of total recruitment by birthweek cohort by year. The temporal range of collections of each birthweek cohort is denoted by a horizontal line and the mode by a closed circle. The peak recruitment density period (highest three consecutive sampling-date catches including the mode) and its percentage in each sampling season is indicated by the bar on the abscissa.

served a similar difference (13-fold) in relative abundances of Atlantic menhaden larvae at Pivers Island between 1966–67 and 1967–68. Their low year (1967–68) estimate was about one half that of the low year (1990–91) estimate in this study. Although relative abundances give estimates of larval recruitment among years, it is not known how representative the estimates are of coastwide year-class strength of the species. Virtual population analyses (VPA) indicate that recruitment to the commercial fishery to age-1 from the 1987–88 year class was about double that of the previous two years, 1985–86 and 1986–87 (Vaughan, 1993). In comparison, the estimate of larval recruitment for 1987–88 was about 3–5 times larger than the 1985–86 and 1986–87 estimates.

An increase in SL of Atlantic menhaden larvae recruited through each of seven seasons has also been observed in earlier studies. Higham and Nicholson (1964) noted that in plankton collections taken in the vicinity of Beaufort, North Carolina, Atlantic menhaden larvae were smallest in December and largest in April. Lewis and Mann (1971) found that the condition factor (weight/length^3) of larval Atlantic menhaden also increased throughout the season. Checkley et al. (1988) showed that the mean SL of Atlantic menhaden larvae about 10 km offshore increased over the period from January 15 to early March. The mean SL of Atlantic menhaden collected by Hettler and Chester (1990) increased from 16.0 mm in November to 27.6 mm in March then decreased to 24.0 mm in April. Similar trends in increasing size of larvae collected throughout the recruitment season have been observed for spot (Allen and Barker, 1990; Flores-Coto and Warlen, 1993), Atlantic croaker, *Micropogonias undulatus* (Allen and Barker, 1990; Warlen and Burke, 1990) and pinfish, *Lagodon rhomboides* (Warlen and Burke, 1990), all species that recruit to the estuary with Atlantic menhaden.

The total time required for transport of larvae from the area of hatching offshore to the estuary can be estimated from the ages of larvae caught at Pivers Island. The observed similarities in patterns of ages over each of the seven recruitment years suggest that similar transport mechanisms operate from year to year. Youngest larvae, which are only recruited at the beginning or end of each season, must be recruited most efficiently to the estuary, while at other times in the season transport becomes less efficient as larvae require longer to get to the estuary. Also, as the season progresses it is likely that spawning may occur further offshore (Warlen, 1992) as suitable spawning temperature water is found farther offshore and, consequently, larvae must be transported a greater distance to estuaries. The extended period of transport allows for mixing of birthweek cohorts offshore as evidenced by the greater mix of birthweek cohorts during the late season recruitment peaks. Mixing could also occur if there is "pooling" of larvae outside the inlet. Warlen (1992) suggested that larval Atlantic menhaden transported from offshore in North Carolina to the estuary was rapid in November–December. However, in the January–March period transport was only rapid to about the mid-shelf frontal zone, after which the overall transport rate was much slower. It is this latter spawned group that apparently makes up the largest fraction of estuarine immigrating larvae each recruitment season.

In summary, during an extended period (fall/winter/early spring) Atlantic menhaden spawn and their larvae are recruited to estuaries in the northern portion of the South Atlantic Bight. Although there is variation, consistent temporal patterns of spawning, recruitment density, and age and size trends are observed from year to year. Back-calculated modes in spawning suggest the importance of short periods within the total spawning season and peaks in estuarine recruitment suggest the importance of larval across-continental-shelf transport and near-shore concentrating mechanisms.

Acknowledgments

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Literature cited

Ahrenholz, D. W., W. R. Nelson, and S. P. Epperly.
1987. Population and fishery characteristics of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull. 85:569–600.

Ahrenholz, D. W., J. F. Guthrie, and C. W. Krouse.
1989. Results of abundance surveys of juvenile Atlantic and gulf menhaden, *Brevoortia tyrannus* and

B. patronus. Dep. Commer., NOAA Tech. Rep. NMFS 84, 14 p.

Allen, D. M., and D. L. Barker.
1990. Interannual variations in larval fish recruitment to estuarine epibenthic habitats. Mar. Ecol. Prog. Ser. 63:113–125.

Atkinson, L. P.
1985. Hydrography and nutrients of the southeastern U.S. continental shelf. *In* L. P. Atkinson, D. W. Menzel, and K. A. Bush (eds.), Oceanography of the southeastern U.S. continental shelf, p. 77–92. Am. Geophys. Union, Wash. D.C.

Bye, V. J.
1990. Temperate marine teleosts. *In* A. D. Munro, A. P. Scott, and T. J. Lam (eds.), Reproductive seasonality in teleosts: environmental influences, p. 125–143. CRC Press, Boca Raton, FL.

Checkley, D. M., Jr., S. Raman, G. L. Maillet, and K. M. Mason.
1988. Winter storm effects on the spawning and larval drift of a pelagic fish. Nature (Lond.) 335: 346–348.

Dryfoos, R. L., R. P. Cheek, and R. L. Kroger.
1973. Preliminary analysis of Atlantic menhaden, *Brevoortia tyrannus*, migrations, population structure, survival and exploitation rates, and availability as indicated by tag returns. Fish. Bull. 71:719–734.

Ferraro, S. P.
1981. Eggs and larvae of Atlantic menhaden (*Brevoortia tyrannus*) in the Peconic Bays, New York in 1972–74. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 178:181–182.

Flores-Coto, C., and S. M. Warlen.
1993 Spawning time, growth and recruitment of larval spot (*Leiostomus xanthurus*) into a North Carolina estuary. Fish. Bull. 91:8–22.

Govoni, J. J.
1993. Flux of larval fishes across frontal boundaries: examples from the Mississippi River plume front and the western Gulf Stream front in winter. Bull. Mar. Sci. 53:538–566.

Hettler, W. F., Jr., and A. J. Chester.
1990. Temporal distribution of ichthyoplankton near Beaufort Inlet, North Carolina. Mar. Ecol. Prog. Ser. 68:157–168.

Higham, J. R., and W. R. Nicholson.
1964. Sexual maturation and spawning of Atlantic menhaden. Fish. Bull. 63:255–271.

Hoss, D. E., L. Coston-Clements, D. S. Peters, and P. A. Tester.
1988. Metabolic responses of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae to cold temperatures encountered following recruitment to estuaries. Fish. Bull. 86:483–488.

Judy, M. H., and R. M. Lewis.
1983. Distribution of eggs and larvae of Atlantic menhaden, *Brevoortia tyrannus*, along the Atlantic coast of the United States. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-774, 23 p.

Kendall, A. W., Jr., and J. W. Reintjes.
1975. Geographic and hydrographic distribution of Atlantic menhaden eggs and larvae along the Middle Atlantic Coast from RV *Dolphin* cruises, 1965–66. Fish. Bull. 73:317–335.

Lambert, T. C., and D. M. Ware.
1984. Reproductive strategies of demersal and pelagic spawning fish. Can. J. Fish. Aquat. Sci. 41:1565–1569.

Lewis, R. M.
1966. Effects of salinity and temperature on survival of larval Atlantic menhaden, *Brevoortia tyrannus*. Trans. Am. Fish. Soc. 95:423–426.

Lewis, R. M., and W. C. Mann.
1971. Occurrence and abundance of larval Atlantic menhaden *Brevoortia tyrannus*, at two North Carolina inlets with notes on associated species. Trans. Am. Fish. Soc. 100:296–301.

Lewis, R. M., D. W. Ahrenholz, and S. P. Epperly.
1987. Fecundity of Atlantic menhaden, *Brevoortia tyrannus*. Estuaries 10:347–350.

Maillet, G. L., and D. M. Checkley Jr.
1990. Effects of starvation on the frequency of formation and width of growth increments in sagittae of laboratory-reared Atlantic menhaden *Brevoortia tyrannus* larvae. Fish. Bull. 88:155–165.

Nelson, W. R., M. C. Ingham, and W. E. Schaaf.
1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull. 75:23–41.

Nicholson, W. R.
1978. Movements and population structure of Atlantic menhaden indicated by tag returns. Estuaries 1:141–150.

Paffenhöfer, G.-A.
1985. The abundance and distribution of zooplankton on the southeastern shelf of the United States. *In* L. P. Atkinson, D.W. Menzel, and K. A. Bush (eds.), Oceanography of the southeastern U.S. continental shelf, p. 104–117. Am. Geophys. Union, Wash. D.C.

Pietrafesa, L. J., G. S. Janowitz, and P. A. Wittman.
1985. Physical oceanographic processes in the Carolina Capes. *In* L. P. Atkinson, D. W. Menzel, and K. A. Bush (eds.), Oceanography of the southeastern U.S. continental shelf, p. 23–32. Am. Geophys. Union, Wash. D.C.

Reintjes, J. W.
1961. Menhaden eggs and larvae from MV *Theodore N. Gill* cruises, South Atlantic coast of the United States, 1953–54. U.S. Fish Wildl. Serv. SSRF-393, Dep. Interior, Bur. Comm. Fish., 7 p.
1969. Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*. U.S. Fish Wildl. Serv. Circ. 320, Dep. Interior, Bur. Comm. Fish., 30 p.

Smith, J. W., W. R. Nicholson, D. S. Vaughan, D. L. Dudley, and E. A. Hall.
1987. Atlantic menhaden, *Brevoortia tyrannus*,

purse seine fishery, 1972–84, with a brief discussion of age and size composition of the landings. Dep. Commer., NOAA Tech. Rep. NMFS 59, 23 p.

Vaughan, D.S.

1993. A comparison of event tree risk analysis to Ricker spawner-recruit simulation: an example with Atlantic menhaden. *In* S. J. Smith, J. J. Hunt, and D. Rivard (eds.), Risk evaluation and biological reference points for fisheries management, p. 231–241. Can. Spec. Publ. Fish. Aquat. Sci., No. 120.

Warlen, S. M.

1992. Age, growth and size distribution of larval Atlantic menhaden off North Carolina. Trans. Am. Fish. Soc. 121:588– 598.

Warlen, S. M., and J. S. Burke.

1990. Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. Estuaries 13:453–461.

Wilkens, E. P. H., and R. M. Lewis.

1971. Abundance and distribution of young Atlantic menhaden, *Brevoortia tyrannus*, in the White Oak River estuary, North Carolina. Fish. Bull. 69:783–789.

Yoder, J. A.

1985. Environmental control of phytoplankton production on the southeastern U.S. continental shelf. *In* L. P. Atkinson, D. W. Menzel, and K. A. Bush (eds.), Oceanography of the southeastern U.S. continental shelf, p. 93–103. Am. Geophys. Union, Wash. D.C.

Yoder, J. A., L. P. Atkinson, S. S. Bishop, E. E. Hofmann, and T. N. Lee.

1983. Effect of upwelling on phytoplankton productivity on the outer southeastern U.S. continental shelf. Continental Shelf Res. 1:385–404.

Abstract.—We used canonical correspondence analysis (CCA), an eigenvector ordination technique that includes direct gradient analysis, to investigate habitat use by spotted, *Stenella attenuata*, spinner, *S.longirostris*, striped, *S. coeruleoalba*, and common, *Delphinis delphis*, dolphins in the eastern tropical Pacific during 1986–90. Data were collected during annual research vessel cruises conducted in August–November of each year. Environmental variables included in the analyses were surface temperature, salinity, sigma-t, and chlorophyll, and thermocline depth and thickness. The dominant pattern in the species-environment relationship (1st canonical axis) separated common dolphins from spotted and spinner dolphins, based on their associations with cool upwelling habitat and warm tropical habitat, respectively. The second axis separated whitebelly spinners from eastern spinner dolphins. Both occurred in tropical water, but were separated primarily by thermocline topography. The species-environment correlations were 0.67 on the first axis, 0.42 on the second. Overall, the environmental data explained 15% of the variance in the species data. For individual school types this ranged from 36% for common dolphins to 6% for striped dolphins. Interannual variability in the species data was small but was judged significant by a Monte Carlo randomization test. Residual interannual variance was insignificant after removing variance associated with environmental variables.

Interannual variability of dolphin habitats in the eastern tropical Pacific. I: Research vessel surveys, 1986-1990

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The eastern tropical Pacific (ETP) supports a diverse and abundant cetacean fauna of over 25 species (Leatherwood et al., 1982; Au and Perryman, 1985). It is a vast area, larger than the entire North Atlantic. Its waters are truly pelagic, except near a few islands and over a narrow continental shelf. Prior to the 1960s almost nothing was known of the distribution and ecology of the region's cetaceans beyond summaries of catch localities from nineteenth century fisheries for large whales (Townsend, 1935).

By the late 1960s, it became clear that large numbers of dolphins were being killed in the ETP in tuna purse seine operations (Perrin, 1969). The U.S. government initiated a program at that time to place scientific observers on purse seiners to monitor dolphin mortality (Smith, 1983). Beginning in 1974, research vessels were dispatched to the region to supplement the observer data (Holt et al., 1987). The combination of these efforts has produced unprecedented amounts of information on pelagic cetaceans. In this study we focused on the dolphin species affected by the tuna fishery: spotted dolphins, *Stenella attenuata*, two subspecies of spinner dolphins, *S. longirostris*, "whitebelly spinners" and "eastern spinners" (Perrin, 1990), striped dolphins, *S. coeruleoalba*, and common dolphins, *Delphinus delphis*.

Dolphin distribution patterns have been described from sighting and collection localities (e.g. Evans, 1975; Perrin, 1975; Perrin et al., 1983, 1985; Au and Perryman, 1985). Au and Perryman (1985) studied cetacean habitats of the eastern tropical Pacific from sightings and oceanographic data collected during the northern winter. They described two complementary patterns, both with apparent links to regional oceanography. One pattern, shown by common and striped dolphins, coincided with "upwelling-modified" conditions found along the equator and at the tropical terminations of eastern boundary currents off Baja California and the coasts of Ecuador and northern Peru (described in more detail below in Study Area). The second pattern, shown by spotted and spinner dolphins, coincided with largely tropical waters off Mexico, where warm, low-salinity surface waters occur over a strong, relatively shallow thermocline.

Reilly (1990) examined ETP dolphin distributions during the northern summer, and quantitatively tested Au and Perryman's habitat hypotheses. He found an apparent offshore shift in spotted, spinner, and striped (but not common) dolphins coincident with seasonal shoaling of a thermocline ridge along 10°N (Fig. 1). This seasonal shoaling is part of the dominant

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pattern of seasonal change in the ETP, associated with the north-south movement of the Intertropical Convergence Zone between the trade winds (Fiedler, 1992). Statistical tests supported the habitat hypotheses of Au and Perryman (1985) for spotted, spinner, and common dolphins, but not for striped dolphins. During the summer, striped dolphins occupied habitat that was geographically complementary with habitats of both common and of spotted/spinner dolphins (Fig. 1). Striped dolphin habitat was indistinguishable statistically from either the upwelling-modified or tropical habitats with the variables used, indicating that other factors or processes act to separate these dolphins from the others.

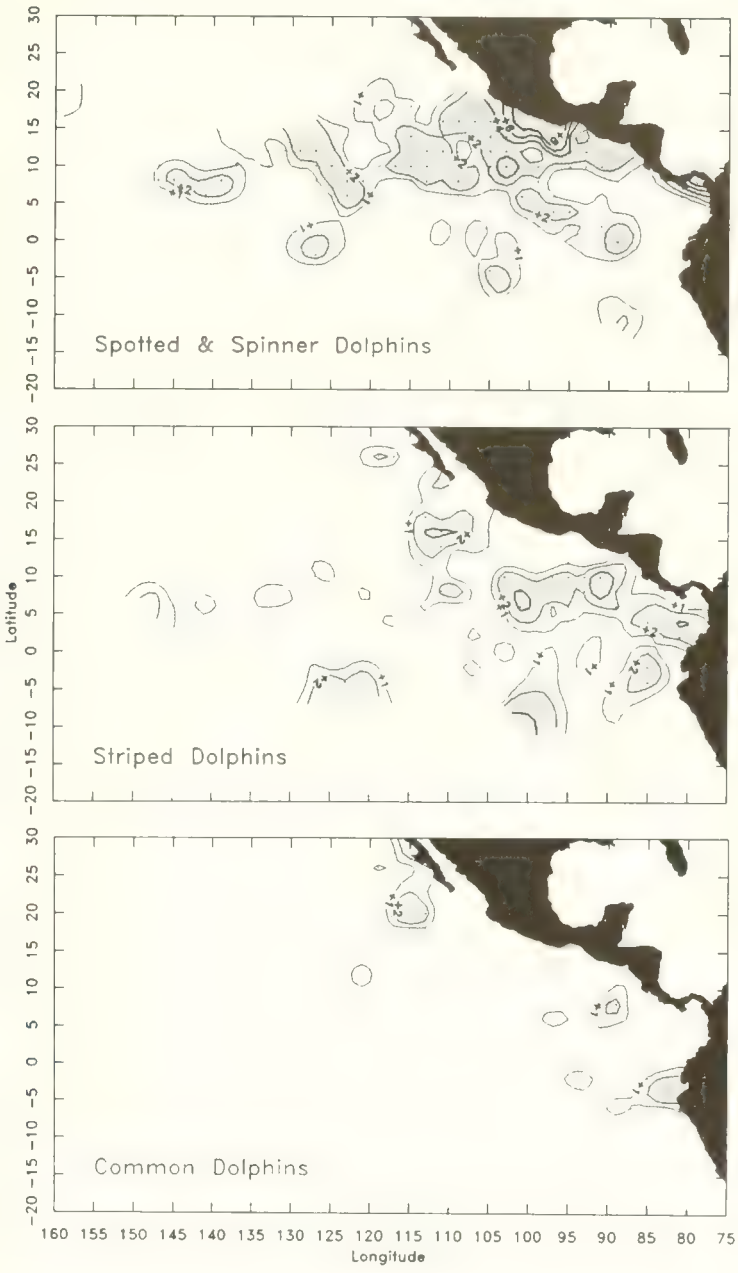


Figure 1

Dolphin distributions in the northern summer in the eastern tropical Pacific, from Reilly (1990). Contours are for encounter rates per 185 km searched. Dots represent centers of 2° squares in which there was at least 185 km search effort.

Interannual variation in the region's oceanography is dominated by the quasi-periodic El Niño-Southern Oscillation (ENSO; Enfield, 1989). Interannual variation exceeds seasonal variation in much of the ETP (Fiedler, 1992). ENSO variability affects all of the patterns and processes so far identified with cetacean habitats in the ETP. From this we hypothesized that dolphin distributions might change interannually in response to changes in the distribution of their habitats. If so, this could have important implications for the monitoring of trends in animal abundance now in progress from research vessel surveys (Gerrodette and Wade, 1991) and tuna vessel observer data (Anganuzzi and Buckland, 1989).

The primary objective of this study was to examine interannual variability in dolphin habitats, defined by multivariate techniques, for the years 1986–90. We also suggest methods for the use of habitat information in the monitoring of trends in cetacean abundance. That is, given a quantitative definition of habitat and a record of interannual changes in habitat distribution, can we help reduce variance or bias, or both, in the estimation of abundance or tests for trends?

Study area

The basic physical features of the upper ocean in the eastern tropical Pacific have been described by Wyrtki (1966, 1967), and Tsuchiya (1974). Fiedler (1992) updated this description and summarized seasonal and interannual variability. Major surface water masses and currents are depicted in Figure 2. Warm, low-salinity tropical surface water is found in the center of the ETP. Cooler, higher-salinity equatorial surface water is found south of about lat.

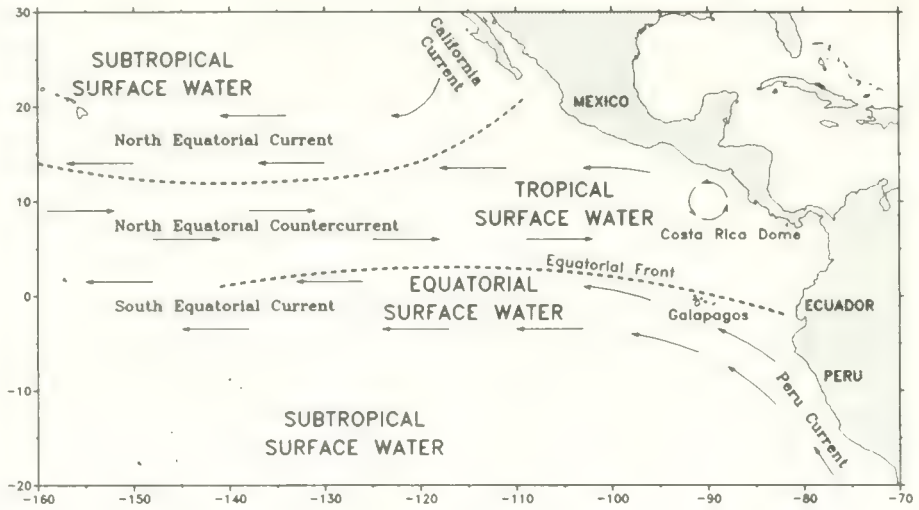


Figure 2

Schematic representation of the surface circulation and water masses of the eastern tropical Pacific.

3°N. Peru Current and California Current Waters are found along the coasts of Peru-Ecuador and Baja California, respectively. The Peru and California Currents feed into the westward South and North Equatorial Currents (SEC, NEC). The North Equatorial Countercurrent (NECC) flows eastward between the NEC and SEC into the center of the Tropical Surface Water mass. The NECC is strong during September–December and weak or absent during February–April.

A permanent shallow thermocline underlies most of the region, shoaling towards the coast (Wyrtki, 1966). Zonal thermocline ridges are found below surface divergences in the SEC along the equator and between the NEC and NECC along lat. 10°N (Fiedler, 1992). Upwelling driven by equatorward longshore winds off Peru and Baja California and by trade winds along the equator brings cold, nutrient-rich water from below the shallow thermocline (nutricline) into the surface layer. This nutrient input maintains optimal (saturating) concentrations of nitrogen at the surface and results in high levels of new production in equatorial and eastern boundary current systems (Chavez and Barber, 1987). Biological productivity is also enhanced by upwelling at the Costa Rica Dome (a quasi-permanent cyclonic eddy at the eastern end of the thermocline ridge along lat. 10°N; Wyrtki, 1964; King, 1986), and by intermittent, topographically induced offshore winds at several points along the coast of Central America (e.g. the Gulf of Tehuantepec, McCreary et al., 1989). Secondary and higher level productivity and standing stocks are generally high in areas of high primary productivity (Blackburn et al., 1970). Within this and other large oceanic regions, the abundance of animals from plankton to large nekton is patchy on a variety of spatial and temporal scales (Haury et al., 1978), with major consequences for the ecology of pelagic predators (e.g. Carr, 1987).

Data and methods

Field data collection

Dolphin sightings and oceanographic data were collected by two ships operating in different parts of the ETP from 28 July through 6 December each year from 1986 to 1990 (e.g. Holt et al., 1987). Track lines are shown in Figure 3. The surveys were conducted at 10 knots (18.5 km/hr) with three observers simultaneously on watch. One observer covered each side of the ship with a pair of 25× binoculars to search an arc from the bow to about 100° to the beam. The third observer covered the track line with hand-held binoculars and the naked eye. Sightings were approached when necessary to allow estimation of numbers within groups and species identification (Holt and Sexton, 1990).

While the ships were underway, surface temperature and salinity were recorded continuously by thermosalinograph (ODEC Model TSG-102, Inter-

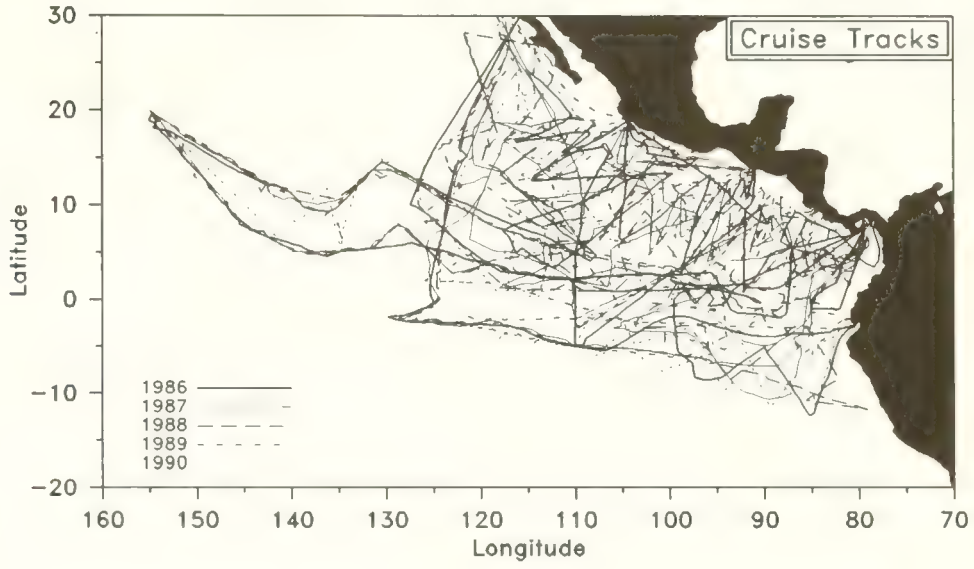


Figure 3

Cruise tracks of RV *David Starr Jordan* and *McArthur* during August–November, 1986–90.

Ocean Model 541, or Seabird SEACAT Model 21). Vertical structure was sampled in two ways. Expendable bathythermographs (XBTs) were deployed four to six times daily (every 55 to 110 km). Twice daily, just before dawn and just after dusk, the ships stopped to deploy conductivity-temperature-depth instruments (CTDs) to 1000 m. Sea water samples were collected with Niskin rosettes for chlorophyll and nutrient analysis. Surface chlorophyll was monitored continuously with a Turner Designs Fluorometer calibrated from discrete samples drawn at the surface at least six times per day (see Fiedler et al., 1990 for details).

The research vessels searched a total of 140,597 km (Fig. 3), and recorded a total of 2,014 sightings of dolphin schools of the seven types considered here, during five annual cruises, 1986 through 1990 (Table 1). The environmental data used include continuous temperature, salinity and fluorescence measurements along most of the trackline, 17,303 surface chlorophyll measurements, 4,726 XBT deployments and 1,596 CTD stations (Table 2).

Analytic methods

We estimated dolphin relative abundance as the number of schools sighted per unit distance searched, for each day, for seven pod-type categories (Table 1). These are the most frequently sighted types of dolphin schools in the region. They are also the types captured by the purse seine fishery. Only days with at least two hours of sighting effort (approximately 37 km) during periods of fair or better sighting conditions (Beaufort 5 or less) were used in the analyses. The distance searched in one day varied between 37 and 222 km. We analyzed daily sightings in relation to environmental conditions measured during that day. Our use of Beaufort 5 as the cut-off follows results from Holt (1987) who analyzed the effects of sea state on dolphin school sightability from ETP ship surveys.

Reilly (1990) found that dolphin habitats in the ETP could be defined statistically by a combination of thermocline depth, surface temperature, and salinity (where temperature and salinity were combined into sigma-t, an index of surface water density, by using a simple linear function described by Pickard and Emery, 1982). We used thermocline depth, surface temperature, salinity, and sigma-t, plus surface chlorophyll (log-transformed), and a measure of thermocline strength (the difference in depth between the 20° and 15° isotherms). Surface temperature, salinity, and chlorophyll were averaged from the day's continuous sampling during sighting effort. Thermocline depth (represented by the depth of the 20°C isotherm: Donguy and Meyers, 1987) and strength were estimated from XBT casts made during or within a few hours of sighting effort. We included sigma-t, in addition to both temperature and salinity, in the multivariate analyses as a form of

Table 1

Search effort and number of cetacean schools recorded by year, 1986–90, from the Monitoring of Porpoise Stocks expedition in the eastern tropical Pacific.

	Year					
	1986	1987	1988	1989	1990	Total
Km. searched	28,917	27,735	24,224	27,323	32,398	140,597
Number of Sightings of						
Spotted dolphins[1]	71	85	47	78	78	359
Common dolphins[2]	57	41	73	59	54	284
Spotted with Eastern Spinner[3]	44	40	33	51	33	201
Spotted with Whitebelly Spinner[3]	33	29	23	24	15	124
Eastern Spinner	27	18	6	19	13	83
Whitebelly Spinner	8	10	18	8	10	54
Striped dolphins[4]	158	180	206	213	152	909
Total sightings used in this analysis	398	403	406	452	355	2014
Other cetacean sightings	501	500	462	512	523	2498
Totals	899	903	868	964	878	4512

[1] *Stenella attenuata.*
[2] *Delphinus delphis.*
[3] *S. longirostris.*
[4] *S. coeruleoalba*

"product variable," to see if it contributed additional information for determining dolphin habitats. In summary, the six oceanographic variables included were 1) surface temperature, TEMP; 2) surface salinity, SAL; 3) surface density, SIGMAT; 4) thermocline depth, Z20; 5) thermocline strength, ZD; and 6) chlorophyll, LOGC.

Table 2

Oceanographic data from the Monitoring of Porpoise Stocks expedition, 1986–90, used in the canonical correspondence analyses. Table entries list numbers of observations for discrete measurements, or number of km covered during continuous measurements. XBT = expendable bathythermograph; CTD = conductivity-temperature-depth.

Data type	1986	1987	1988	1989	1990	Total
Surface temperature, salinity (km)	28,917	27,735	24,224	27,323	32,398	140,597
Surface chlorophyll measurements	3,763	1,927	3,613	3,552	4,448	7,303
XBT measurements (drops)	1,144	1,160	835	778	809	4,726
CTD measurements (stations)	244	280	352	352	368	1,596

We examined the effects of interannual variability by including years (scaled 1–5) as categorical variables (details below). Additionally, we examined the contribution of fixed geographic effects by including latitude and longitude in some analyses. All environmental variables (oceanographic and geographic) were normalized prior to multivariate analyses to remove effects from differing scales of measurement.

Relationships between dolphin school distributions and environmental variation were analyzed by using canonical correspondence analysis (CCA; Ter Braak, 1986). We used the computer program CANOCO (Ter Braak, 1985). Correspondence analysis is an eigenvector ordination technique, similar to principal components analysis, that can be used to investigate community structure. These methods extract dominant, orthogonal axes of variation in abundance indices for multiple species at multiple sites. Typically, the ordination axes are then interpreted indirectly with the help of external knowledge and data on environmental gradients, either qualitatively or with regression methods (Gauch, 1982).

In contrast to principal components analysis and other linear methods, correspondence analysis (CA, also called reciprocal averaging) fits nonlinear Gaussian (unimodal) models to the species abundance data. Canonical correspondence analysis is an extension of CA in which the species ordination is done directly and iteratively in relation to environmental variables. CCA is an efficient ordination tech-

nique when species have bell-shaped response curves or surfaces with respect to environmental gradients (Ter Braak, 1986), which is consistent with general ecological knowledge (e.g.Whittaker et al., 1973). The models and algorithm used in the CANOCO implementation of canonical correspondence analysis are documented in Ter Braak (1986).

As part of the species-environment ordination, CCA estimates a series of site scores (here, site=day) that are linear combinations of the environmental variables that maximize the species-environment correlation. One set of site scores is estimated for each canonical ordination axis. The interpretation of environmental patterns represented by the axes is made from the correlation coefficients and the multiple regression or "canonical" coefficients of the original environmental variables with the canonical axes (Ter Braak, 1986).

The results of canonical correspondence can be best interpreted from an ordination "biplot," on which species and sites can be represented by points and environmental variables by arrows. The biplot displays the mean species scores or "optima" on two canonical axes, usually the first two, which explain the majority of the variance. The directions and relative lengths of the arrows for environmental variables represent their contributions to the ordination. More important environmental variables are therefore represented by longer arrows. In making biplots we used Hill's scaling (Ter Braak, 1986) in which site scores were computed as weighted averages of species scores (S=–1 in our implementation of CANOCO).

Community ordination was not our primary objective, but we used CCA for three reasons. It provides a quantitative definition of habitat for each species/stock in reduced dimensionality. The method estimates habitats using a nonlinear, unimodal model, avoiding the unrealistic assumption of a linear relationship between animal abundance and environmental gradients. CANOCO is also insensitive to a high frequency of zero observations (Ter Braak, 1985), typically found in animal survey data.

In assessing the contributions of environmental variables we took the liberal approach of retaining variables unless their contribution to the ordination was almost entirely encompassed by other, more influential variables. That is, a variable of marginal significance was not excluded if the apparent direction of its influence was different from the other environmental variables. Precision in estimating canonical coefficients was not compromised by retaining these marginal variables because we had 956 cases and a maximum of only 13 environmental variables (considering years as five dummy variables). We did not use stepwise procedures, which appear to offer an objective approach to variable selection, but are notoriously problematic for other reasons (e.g. Pimentel, 1979, p. 42–43).

We examined the importance of interannual variability in two related ways. First, as noted above, we included years as categorical explanatory variables, in addition to the oceanographic variables. The importance was then gauged by comparing ordination results to those with just the oceanographic variables. Second, we removed the variance associated with the environmental variables (by defining them as covariables), and then extracted axes associated with variance among years, to test for interannual differences in the species data not associated directly with interannual environmental variation.

The significance of an ordination axis was determined by testing the null hypothesis that its eigenvalue was not different from zero. The procedure used was a Monte Carlo randomization test (e.g. Hope, 1968) supplied with the program CANOCO. This procedure randomly associated sets of environmental variables from one case with sets of species data from another, then extracted canonical axes, and estimated their eigenvalues. The procedure was run 1,000 times to produce a reference set of eigenvalues representing random variability. The significance of the eigenvalues from the original data was determined by comparison to these distributions.

We extended the use of canonical correspondence analysis in two ways for our study of interannual variation in cetacean habitats. First, we mapped the spatial distributions of the site scores from the first two CCA axes, lightly smoothed and contoured. We then plotted the localities of cetacean sightings over these contours to allow visual appraisal of species-environment patterns. We did this as an alternative to plotting species and hundreds of sites together on a biplot, which we found to be uninformative. Second, we suggest two ways in which the results of the canonical correspondence analysis can be used in the monitoring of trends in cetacean abundance.

Results

Table 3 gives the weighted correlation matrix for the six oceanographic variables, the four species axes and four environmental axes from the CCA. The "species-environment" correlations are the values for equivalent axes, e.g. the correlation between the dominant species axis (no. 1) and the first environmental axis is 0.67. The correlation between the second axes is 0.42, and so on.

The ordination including the six oceanographic variables explained 14.7% of the variance in the dol-

Table 3

Correlation coefficients among environmental variables, canonical species axes and environmental axes estimated by a canonical correspondence analysis of cetacean abundances in the eastern tropical Pacific during 1986–90. Values marked with an * are significantly different from zero at a $P \leq 0.05$.

	SPECAX1	SPECAX2	SPECAX3	SPECAX4	ENVIAX1	ENVIAX2	ENVIAX3	ENVIAX4	TEMP	SAL	LOGC	SIGMA T	Z20
SPEC AX1	1.0000												
SPEC AX2	0.0085	1.0000											
SPEC AX3	0.0046	−0.0523	1.0000										
SPEC AX4	0.0283	0.0916	−0.0078	1.0000									
ENVI AX1	0.6692*	0.0000	0.0000	0.0000	1.0000								
ENVI AX2	0.0000	0.4152*	0.0000	0.0000	0.0000	1.0000							
ENVI AX3	0.0000	0.0000	0.1957	0.0000	0.0000	0.0000	1.0000						
ENVI AX4	0.0000	0.0000	0.0000	0.1196	0.0000	0.0000	0.0000	1.0000					
TEMP	−0.5885*	0.1445	−0.0143	0.0197	−0.8794*	0.3481*	−0.0730	0.1650	1.0000				
SAL	0.0599	−0.1110	0.0396	−0.0395	0.0895	−0.2674*	0.2022	−0.3304*	−0.4747*	1.0000			
LOGC	0.3246*	0.1354	−0.0803	−0.0721	0.4850*	0.3260*	−0.4106*	−0.6023*	−0.3697*	−0.0209	1.0000		
SIGMA T	0.4054*	−0.1646	0.0172	−0.0333	0.6058*	−0.3964*	0.0879	−0.2781	−0.8892*	0.8186*	0.2280	1.0000	
Z20	−0.4702*	−0.2630*	0.0239	0.0036	−0.7026*	−0.6336*	0.1224	0.0296	0.3921*	0.0811	−0.5103*	−0.2032	1.0000
ZD	0.2993*	0.0152	−0.0347	0.0788	0.4472*	0.0366	−0.1774	0.6588*	−0.3560*	0.0205	0.0476	0.2286	−0.2032

phin school abundance data as a whole, with a range from 33.5% for common dolphins to just 5.1% for whitebelly spinner dolphins (Table 4). The eigenvalues for the ordination axes indicate that only the first two are important (Table 4). Axes 3 and 4 together represent only 6% of the variation of the species—environment data. Ter Braak (1985) suggests that eigenvalues less than 0.02 be disregarded. The first axis accounts for 70% of the variance extracted, the second accounts for 24%, together they represent 94%. Further results and discussion therefore relate primarily to axes 1 and 2.

The relationships between most of the species categories of interest and the first two environmental axes were unimodal (Fig. 4), satisfying a primary assumption of CCA. One exception was common dolphins on axis 1, where there is evidence of bimodality.

The Monte Carlo randomization test resulted in rejection of the null hypothesis of no relationship between the species encounter rates and the environmental data (H_0: $\lambda=0$). One thousand random permutations produced no ordinations with a trace (eigenvalue total) larger than the observed 0.443, giving a

Table 4

Ordination results from a canonical correspondence analysis of dolphin abundance and oceanographic conditions (surface temperature, salinity, sigma-t, chlorophyll, thermocline depth and thermocline strength) in the eastern tropical Pacific, August–November, 1986–90. "S-E total" is the sum of the species-environment eigenvalues, i.e. the species variation related to the environmental variables. "Overall total" is the total of all variation in the species encounter rate data. *P*-values are from a Monte Carlo randomization test with 1,000 repetitions.

	Canonical axes				S-E	Overall
	1	2	3	4	total	total
Eigenvalues	0.309	0.107	0.020	0.005	0.443	3.002
P-values	<0.001				<0.001	
Species-environment correlations	0.669	0.415	0.196	0.120		
Cumulative percentage variance						
species-environment relation	69.8	93.9	98.4	99.5		
total species data	10.3	13.8	14.5	14.7		
spotted dolphin[1]	7.9	7.9	8.1	8.1		
common dolphin[2]	33.7	34.9	35.5	35.5		
spotted and eastern spinner[3] dolphins	13.1	22.2	22.3	22.5		
spotted and whitebelly spinner[3] dolphins	8.3	9.3	9.5	9.7		
eastern spinner dolphin	6.6	7.4	7.4	8.3		
whitebelly spinner dolphin	0.9	3.7	4.8	5.1		
striped dolphin[4]	1.7	2.8	5.9	5.9		

[1] *Stenella attenuata*
[2] *Delphinus delphis*
[3] *Stenella longirostris*
[4] *S. coeruleoalba*

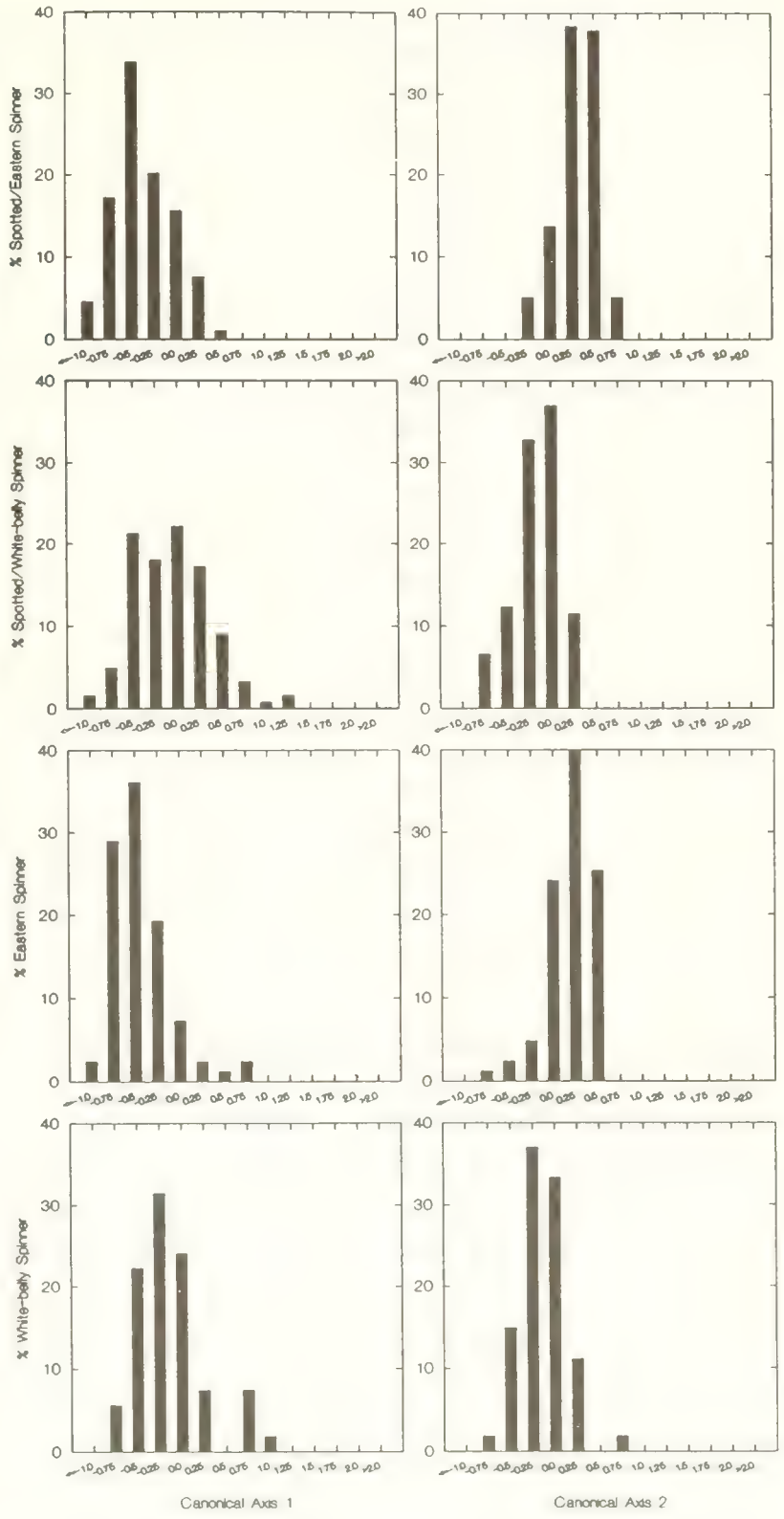


Figure 4

Frequency histograms, transformed to percentages, of the first two environmental axis scores in areas where cetaceans were sighted for seven species/stocks.

P-value < 0.001. The same was true for the first axis alone; no random permutation had an eigenvalue larger than the observed 0.309, again giving a *P*-value < 0.001. These results indicate that the probability of a Type-I error is less than 0.1%. (The CCA program, CANOCO, provided this test only for the trace and first axis, so no test was done for subsequent axes).

The species-environment biplot (Fig. 5A) displays the results for the six variable 'oceanographic' ordination. Fig. 5B shows the ordination with species tolerances, but without the visual distraction of the environmental vectors. The first axis separates common dolphins from all school types containing spotted and spinner dolphins. Positive scores on axis 1 are associated with cooler temperature (r=–0.88, Table 3), a thermocline that is shallower (i.e. smaller Z20, r=–0.70), yet weaker (larger difference in depth between 20° and 15°C isotherms, r =+0.45), denser surface water (higher sigma-t, r=+0.61) and high chlorophyll (r=+0.49). These are characteristics of "cool upwelling" habitat, as found in Equatorial and Peru/California Current surface waters. The distinct placement of common dolphins in the positive region of this axis indicates this is their preferred habitat. Negative scores on axis 1 are associated with warm temperature, a deeper and stronger thermocline, and lower chlorophyll, as found in less productive Tropical Surface Water. The placement of all spotted and spinner school types in the negative region indicates that these oceanographic conditions help define their preferred habitats.

Site or species scores on axis 2 are uncorrelated with scores on axis 1, by definition. Positive axis-2 scores are associated with a relatively shallow thermocline (r=–0.63, Table 3) and high chlorophyll (r=+0.40) as for axis 1, but also with warmer temperatures and lower salinity (lower sigma-t) rather than cool

temperature. These are characteristics of "coastal tropical" habitat found along the coast of Central America, where the surface layer is more stratified and upwelling is more intermittent and localized than in the cool upwelling habitat. Whitebelly spinners, alone and with spotted dolphins, had large negative axis-2 scores, while eastern spinners with spotted dolphins had positive scores. There was a strong separation on axis 2 between mixed schools of whitebelly spinners with spotted dolphins, and schools of eastern spinners with spotted dolphins. Schools of spotted dolphins alone had near-zero axis 2 scores. Striped dolphins loaded near the origin of both axes.

The spatial distributions of yearly axis 1 scores are mapped in Figure 6. Areas with positive scores are shaded to allow quick appraisal of changes between years (interpreted below). Also plotted in Figure 6 are sighting localities for spotted and common dolphins. Spotted dolphins occurred mostly in negative areas, common dolphins in positive areas, but with some overlap.

Spatial distributions of yearly axis 2 scores are mapped in Figure 7, with positive scores shaded. Whitebelly spinners occurred almost exclusively in waters with negative axis-2 scores (Figs. 5 and 7). Eastern spinners ranged throughout both positive and negative areas; a modest majority were found in positive areas. They were less closely associated with this axis than whitebelly spinners (Fig. 5) and seemed to be found in the eastern (more coastal) part of the warm tropical habitat defined by negative axis-1 scores.

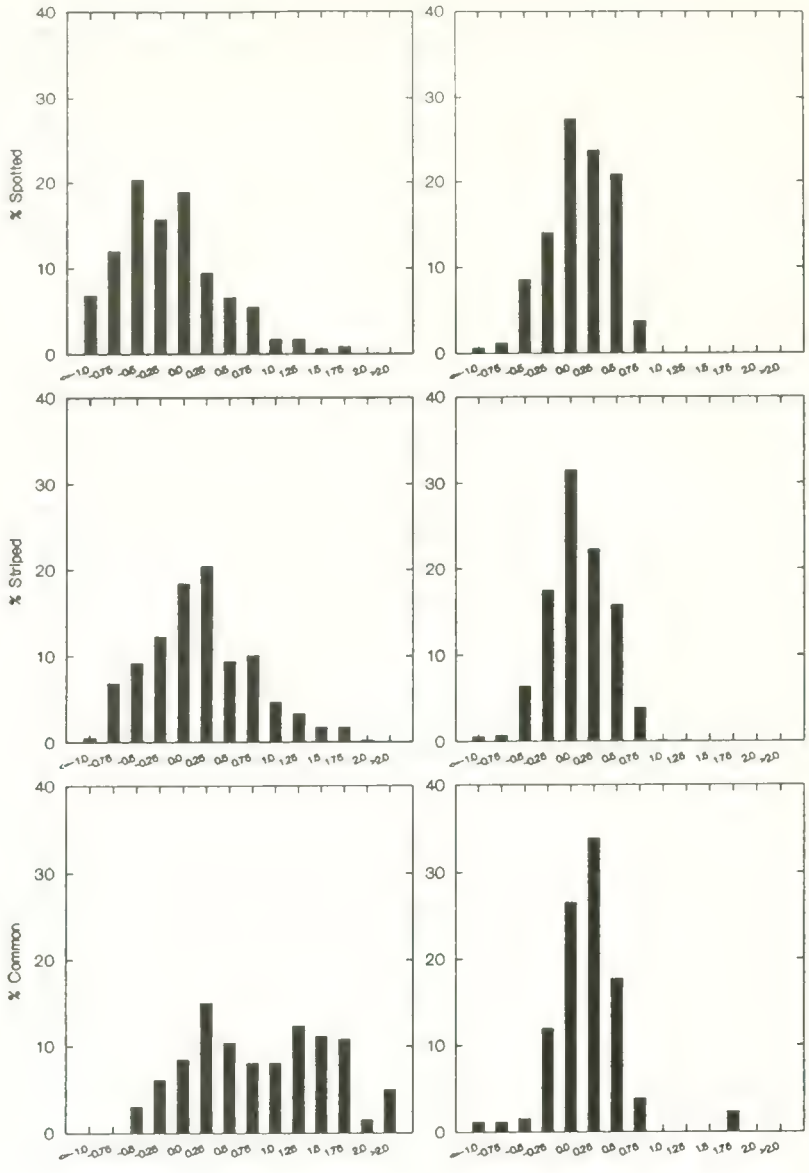


Figure 4 (Continued)

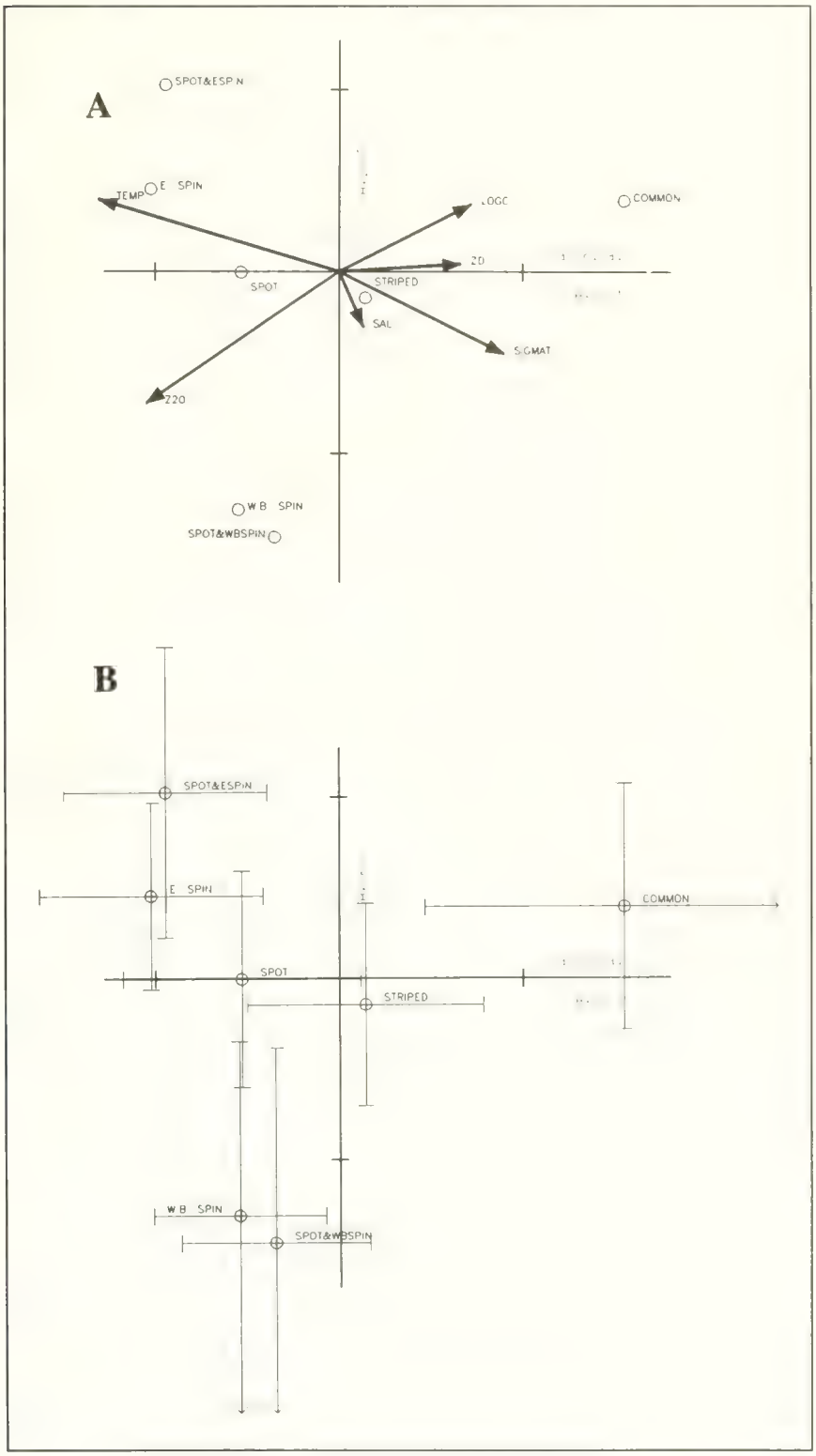
Interannual variability

We obtained only a slight increase in the percent of variance explained for the dolphin data (14.7% to 15.1%, Table 5) from addition of categorical variables representing the five sampled years, in addition to the six oceanographic variables. An ordination biplot from this analysis (Fig. 8) shows that the centroid for 1988 (year 3) loads farthest from the origin. Its location represents the cooler, more productive conditions associated with the 1988 La Niña.

An analysis including just years as categories, without oceanographic variables, explained only about 2% of the dolphin variance, but the dominant eigenvalue and trace were both significantly different from zero (Monte Carlo P-values=0.01 and 0.02, respectively). After extraction of the variance associated with the six oceanographic variables (by defining them as covariables) the ordination was not significant (Monte Carlo P=0.058, Table 5).

Fixed geographic effects

Inclusion of latitude and longitude in addition to the six oceanographic variables produced a notable increase in dolphin variance explained, from 14.7% to 20.5% (Table 5). The amount of additional influence indicated for fixed geographic effects varied substantially among school types. The largest increases were for whitebelly spinners, alone and with spotted dolphins. No improvement in explaining variance was made for schools of spotted dolphins alone.



Group size effects

This study used encounter rates as an index of abundance. This index does not encompass effects of varying group size. There is some evidence for geographic patterns in group size for the dolphin school types studied (Gerrodette and Wade, 1991), so the analyses reported here were also run with the dependent variables modified as follows. Encounters with schools were weighted by the number of individuals estimated to be in the school. The weighted rate was then log-transformed. Canonical correspondence analyses run with these modified dependent variables produced essentially the same patterns as before, but with a small loss of explanatory power: the cumulative percent of the species variance explained was 14.2%, down from 14.7%.

Discussion

Species-environment patterns

The ordination results were generally consistent with past studies of

Figure 5

Ordination results from canonical correspondence analysis of cetacean species/stocks and environmental conditions in the eastern tropical Pacific. (**A**) Biplot of first two canonical axes and environmental variables. (**B**) Ordination showing 95% confidence limits for the species loadings. The environmental variables, represented by arrows in 5A, are surface temperature (TEMP), surface salinity (SAL), thermocline depth indexed by 20°C isotherm depth (Z20), thermocline strength, indexed by the difference in depth between the 20°C and 15°C isotherms (ZD), surface water density (SIGMAT), and surface chlorophyll, log-transformed (LOGC). These two axes represent 94% of the species-environment variance, 15% of the total encounter rate variance.

ETP cetacean ecology. The first axis contrasts the habitat use of common dolphins with spotted and spinner dolphins. The placement of common dolphins into cool upwelling habitat is consistent with results reported by Au and Perryman (1985) and Reilly (1990). The placement of spotted and spinner dolphins in contrasting habitat (negative axis-1 values; essentially warm tropical water) is also as reported earlier. Consistency with results of Reilly (1990) is not surprising, because that study shared data from 1986 and 1987 with this study, but is somewhat reassuring because different analytical techniques were used.

The second axis separated eastern spinners from whitebelly spinner dophins. This separation was even clearer between sightings of eastern spinners mixed with spotted dolphins and whitebelly spinners mixed with spotted dolphins. The ordination placement of whitebelly spinner dolphins in habitat with a deeper thermocline (negative axis 2) follows from their more offshore distribution and the general tendency for the thermocline to become deeper to the west in the ETP. Spotted dolphins alone occurred intermediate to these mixed schools. If this is a general pattern it suggests that the two mixed-school types of spotted and spinner dolphins are utilizing habitats as different as those used by separate species (e.g. common dolphins and spotted dolphins on axis 1). These results are consistent with the hypothesis that the morphological distinctness of the endemic eastern spinner dolphin subspecies reflects adaptation to local habitat conditions (Dizon et al., 1991), and the recent finding that spotted dolphins north of the equator and east of long. 120°W, i.e. those available to school with eastern spinner dolphins, comprise a distinct 'stock' (Dizon et al., in press).

The ordination of striped dolphins near the origin of both axes 1 and 2 indicates either that this is near their optimum habitat or that their distribution is unrelated to the environmental patterns represented in the canonical axes. The low "R^2" for striped dolphins (Table 4), and their widespread spatial distribution (Fig. 1; Reilly, 1990) support the latter interpretation.

The species-environment correlations observed were quite high: 0.67 for the first species and environment axes, 0.42 for the second axes. However, variation extracted by the canonical correspondence analysis accounted for just 15% of the total encounter rate variance. (This was increased to over 20% when fixed geographic effects were considered.) This modest explanatory power is in fact fairly good, given the unknown but surely large sampling variability inherent in daily encounter rates, and is consistent with levels of explanatory power in similar CCA analyses of abundance data (e.g. Ter Braak, 1986). Dolphins are very mobile and patchily distributed large predators, and are known to have complex social and behavioral interactions with their own and other species. These characteristics combine to produce highly variable abundance indices.

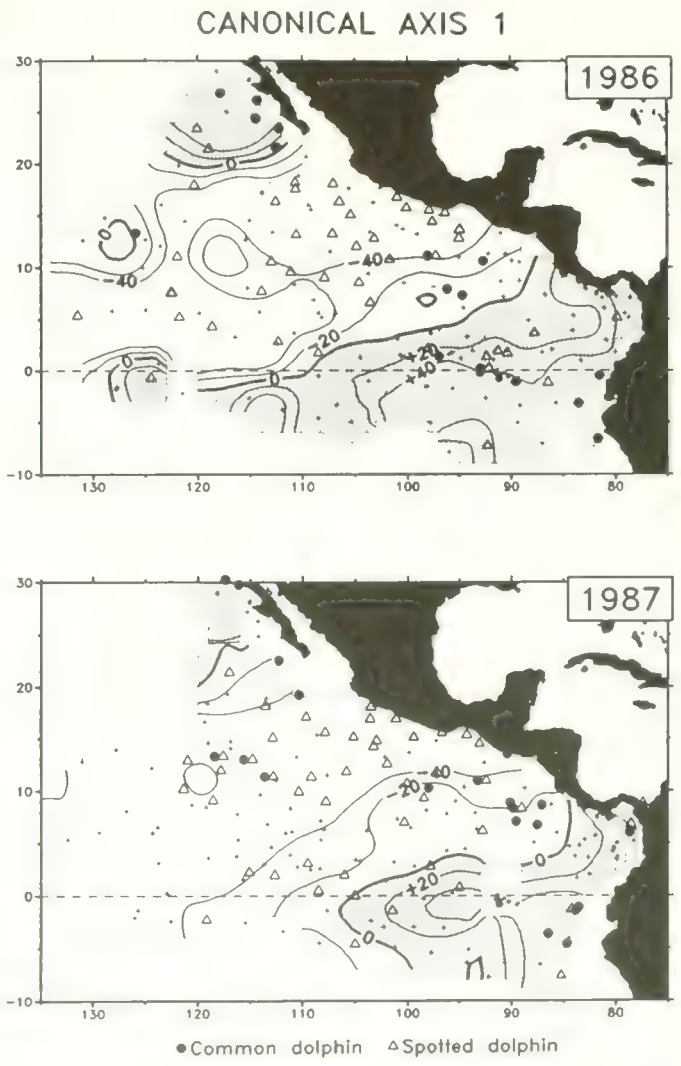


Figure 6

Maps of distribution of canonical axis 1 for 1986–90. Positive areas are shaded. Spotted dolphin, *Stenella coeruleoalba*, sighting localities are shown as open triangles, common dolphin, *Delphinus delphis*, localities as closed circles. A "+" represents a sighting day during which neither spotted nor common dolphins were seen.

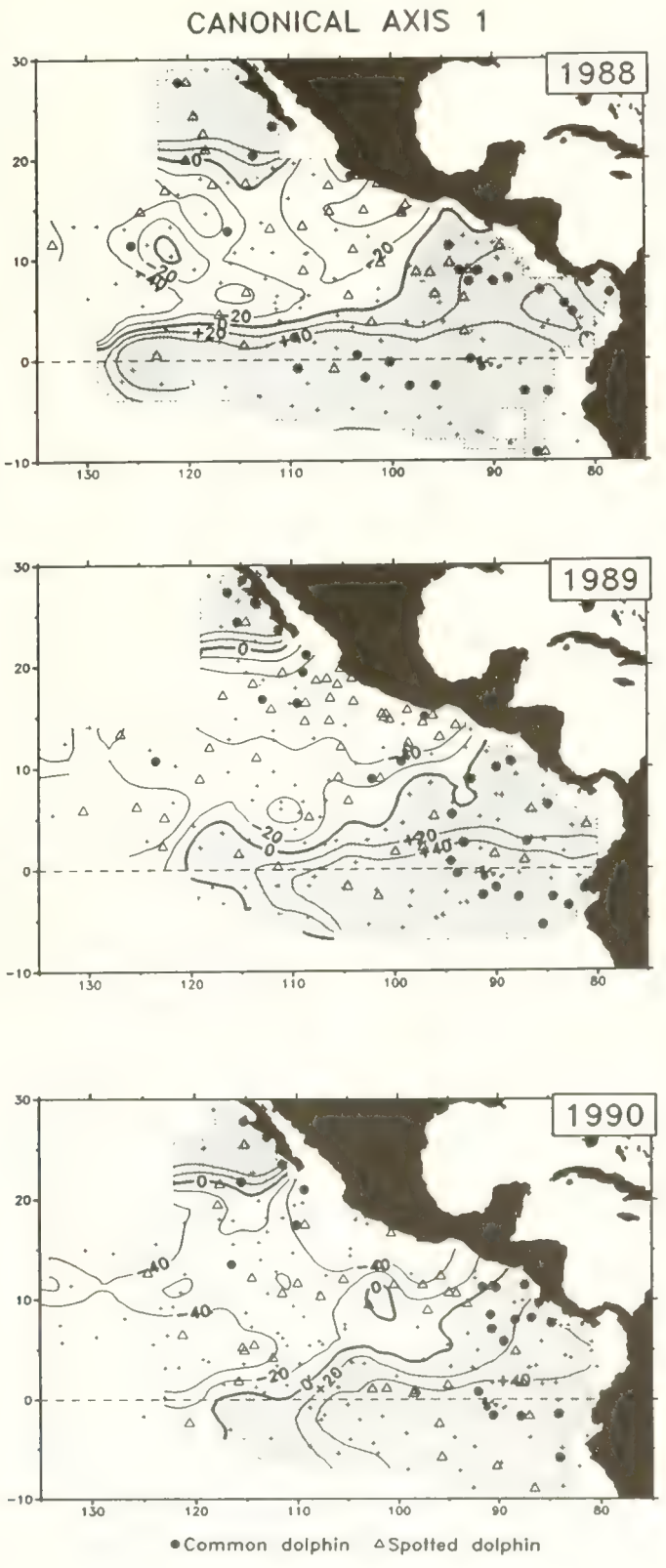


Figure 6 (Continued)

Explanatory power for common dolphins was surprisingly high: 36% with the six oceanographic variables, and 42% with fixed geography included. This result indicates that common dolphins have the tightest association with the environmental variables of the seven school types studied here. It also demonstrates the robustness of CCA, considering the bimodal distribution of common dolphins on axis 1 (Fig. 4).

The notable increase in performance for whitebelly spinner dolphins resulting from consideration of fixed geography raises interesting questions. Are they directly responding to some geophysical cue, such as magnetic anomalies (Kirschvink et al., 1986; Klinowska, 1985)? Or, does this result simply reflect orientation to oceanographic features or processes (e.g. prey distribution) not represented in our data?

Interannual variability

Interannual environmental variability is apparent in the geographic distributions of the canonical axis scores, and to a lesser extent in locations of dolphin sightings (Figs. 6 and 7). In 1986, cool upwelling habitat was found along the equator to long. 130°W, north of the equator to about lat. 10°N along the coast of Central America, and off the coast of Baja California. In 1987, cool upwelling habitat south of Baja California did not extend west of 110°W or north of 4°N, except in the Gulf of Panama. The study area was dominated by warm, low-productivity tropical water (negative axis-1 scores). This change was caused by a moderate El Niño event that began in late 1986 and lasted through 1987 (Kousky and Leetmaa, 1989). In 1988, cool upwelling water extended far north of the equator and south of Baja California, considerably reducing the area covered by tropical water. 1988 was a strong anti-El Niño or La Niña year (Leetmaa, 1990; Fiedler et al., 1992). In 1989 and 1990, conditions represented by axis-1 scores returned to a state similar to 1986. Interannual variation along axis 2 was not strongly related to ENSO variability. The area with positive axis-2 scores ("coastal tropical" habitat) was small in 1986 and 1987, increased in 1988 and again in 1989, and showed some diminishment in 1990.

Common dolphin distribution was previously observed to show no apparent seasonal changes (Reilly, 1990) but was observed here to change interannually more than the other school types studied, and these changes appear related to

ENSO variability. In 1987, with "cool upwelling" conditions contracted eastward and southward at the equator as part of that year's El Niño, in the southern ETP (south of about 2°S) common dolphins occurred only in the far east off South America. In 1988 during the strong La Niña these conditions were well established along the equator to the western extent of the study area, and common dolphins occurred in equatorial waters as far west as 110°W.

The maps in Figures 6 and 7 are imprecise representations of species-environment patterns derived by CCA for two reasons. First, the maps show only presence-absence, while we used an effort-corrected index of abundance (daily encounter rate) in the CCA. Second, the contouring requires some smoothing and interpolation between sites, while the CCA compared abundance indices only to environmental variables measured during the same day, along the same track lines where the cetaceans were sighted. These species are apparently separating more strongly on a smaller scale than we could effectively represent on the maps. A further consideration is that the scaling of axes for biplot presentation was done by using a method in which the canonical scores (as plotted on the maps here) are rescaled to produce biplot locations (Ter Braak, 1988). The resulting ordination gives an accurate relative placement of species centroids, but does not allow direct projection of centroids or tolerances onto canonical axis values as mapped in Figures 6 and 7.

The small but significant interannual variation in the species data was effectively accounted for by interannual variation in the environment. This was demonstrated by the low eigenvalue (λ=0.02, P=0.06) for interannual differences after extracting variance associated with the six oceanographic variables. This result does not necessarily apply to total population abundances, however, because in the above analyses we did not include school size estimates in our species data.

Group size effects

Inclusion of group-size data in the dolphin abundance index produced ordinations that were very similar to those using simple encounter rates, but with a slight decrease in explanatory power from the environmental data. We interpret this result to indicate that schools of all sizes occupy approximately the same habitats, and that school size variability within these habitats is not strongly related to the environmental variables analyzed here.

Applications to dolphin assessments

We suggest two approaches to use the results of this study in cetacean abundance and trend monitoring.

Table 5

Comparative ordinations from canonical correspondence analyses of seven types of dolphin school in the eastern tropical Pacific, with six different sets of environmental variables. Set 1 = surface temperature (SST), thermocline depth (Z20) and thermocline strength (ZD). Set 2 = SST, Z20, ZD, surface salinity (SAL), surface chlorophyll (LOGC) and surface density (SIGMA-T). Set 3 = Set 2 plus years (1–5) as categorical variables. Set 4 = Set 2 plus latitude and longitude. Set 5 = Set 2 plus both latitude & longitude and years. Set 6 = years (1–5) as categorical variables, after removing variance associated with all other environmental variables (Set 5).

	Environmental variable set					
	1	2	3	4	5	6
Eigenvalue sum	0.384	0.443	0.464	0.622	0.644	0.022
P-value	<0.001	<0.001	<0.001	<0.001	<0.001	0.058
Percent variance accounted for						
total species data	12.8	14.7	15.1	20.5	21.1	0.9
spotted dolphin[1]	7.8	8.1	8.8	8.8	9.6	0.8
common dolphin[2]	32.6	35.5	36.2	41.2	42.2	1.0
spottted and eastern spinner dolphins[3]	18.8	22.5	22.8	25.0	25.3	0.3
spotted and whitebelly spinner dolphins[3]	9.2	9.7	9.9	16.4	17.3	1.0
eastern spinner dolphin	7.5	8.3	9.5	10.4	11.2	0.9
whitebelly spinner dolphin	3.6	5.1	6.4	20.0	20.3	0.3
striped dolphin[4]	1.9	5.9	6.6	12.6	13.8	1.9

[1] *Stenella attenuata.*
[2] *Delphinus delphis.*
[3] *S. longirostris.*
[4] *S. coeruleoalba.*

Other, perhaps more sophisticated approaches are possible. We present these only as examples. The most straightforward approach, involving minimal assumptions, would be to post-stratify the data for each year separately, based on the spatial distribution of CCA axis scores and the weighted mean and standard deviation of those scores for the species of interest. This would be done to improve precision of abundance estimates. Populations that have similar means and standard deviations could use common strata. For example, separate strata could be defined by using axis 1 for common and spotted dolphins. Axis 2 could be used to provide strata for whitebelly spinner dolphins. Because we have probability distributions for the occurrence of these species along the canonical axes, we would not be limited to use just two strata but could use three or four. After the data were stratified based on the species annual habitat distributions, standard line transect methodology would be followed. This is generically similar to the post-stratification approach taken by Anganuzzi and Buckland (1989) to reduce bias in estimates of dolphin abundance from tuna vessel observer data.

A second possible approach, aimed at improving accuracy, would quantify the amount of habitat available within the study area each year, for each population. The simplest quantification scheme would define only two strata for each. The cut-point between strata could be the 95% limit of the population's distribution on the axis, or, less conservatively, the appropriate upper or lower quartile. More complex schemes using more than two strata could be developed, as with the post-stratification, based on additional information in the species probability distributions. The amount of any stratum available in a year could be quantified by, say, lightly smoothing and interpolating the CCA site scores (to provide values for all locations) and "sampling" the distribution with the actual cruise tracks for the year. If for example common dolphin habitat was to be defined as axis 1 > [some value], the amount of ocean sampled with axis 1 > [some value] in 1986 could be scaled as 1.0. The amount sampled in subsequent years could be scaled to the 1986 amount. The result would be a vector of values representing the amount of common dolphin habitat available within the ETP by year. This vector could then be applied to the encounter rate portion of the line transect abundance estimate for each year to account for changing availability of common dolphin habitat. If interannual differences were subsequently observed in the line transect abundance estimates, we could be more confident that they represent real changes in abundance, rather than just apparent changes due to spatial redistribution relative to sampling effort following habitat shifts.

In a separate study (Fiedler and Reilly, 1994) we applied the CCA ordination approach developed here to investigate interannual variability in abundance indices for ETP dolphins estimated from tuna vessel observer data. We calculated annual indices of habitat quality for each dolphin species targeted by the tuna fishery, for the years 1975–90, then compared these

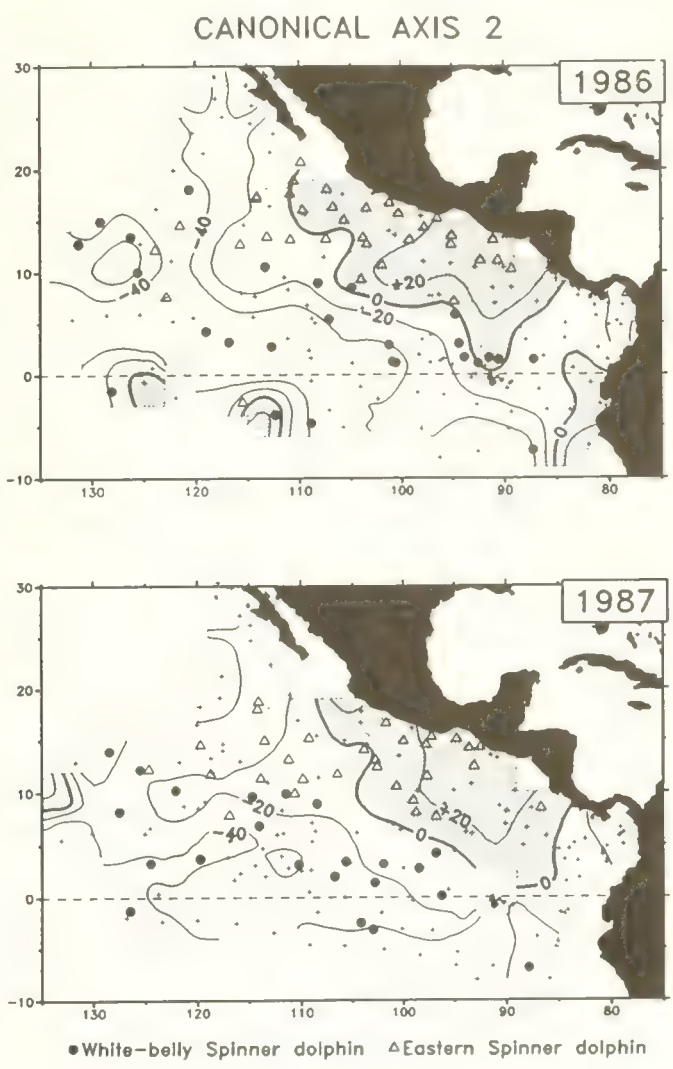


Figure 7

Maps of distribution of canonical axis 2 for 1986–90. Negative areas are shaded. Eastern spinner dolphin, *Stenella longirostris*, sighting localities are represented by closed circles, whitebelly spinner dolphin, *S. longirostris*, localities by open triangles.

habitat indices to Anganuzzi et al.'s (1991) abundance estimates. We used a subset of three environmental variables from those used here, to enable use of existing, large data bases on oceanography of the ETP, to allow computation of environmental axes for years prior to 1986. We found that, for some species, environmental variability does appear to influence abundance estimates made from tuna vessel observer data. We are now working on using environmental data to reduce error in dolphin abundance estimates derived from both research vessel and tuna vessel sightings data. Gerrodette et al.[1] applied the results of this study in a preliminary attempt to account for movements in and out of the study area when estimating total abundance of dolphins.

Acknowledgments

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[1] Gerrodette, T., P. C. Fiedler, and S. B. Reilly. 1991. Including habitat variability in line transect estimation of abundance and trends. NOAA-NMFS Admin. Rep. LJ-91-37.

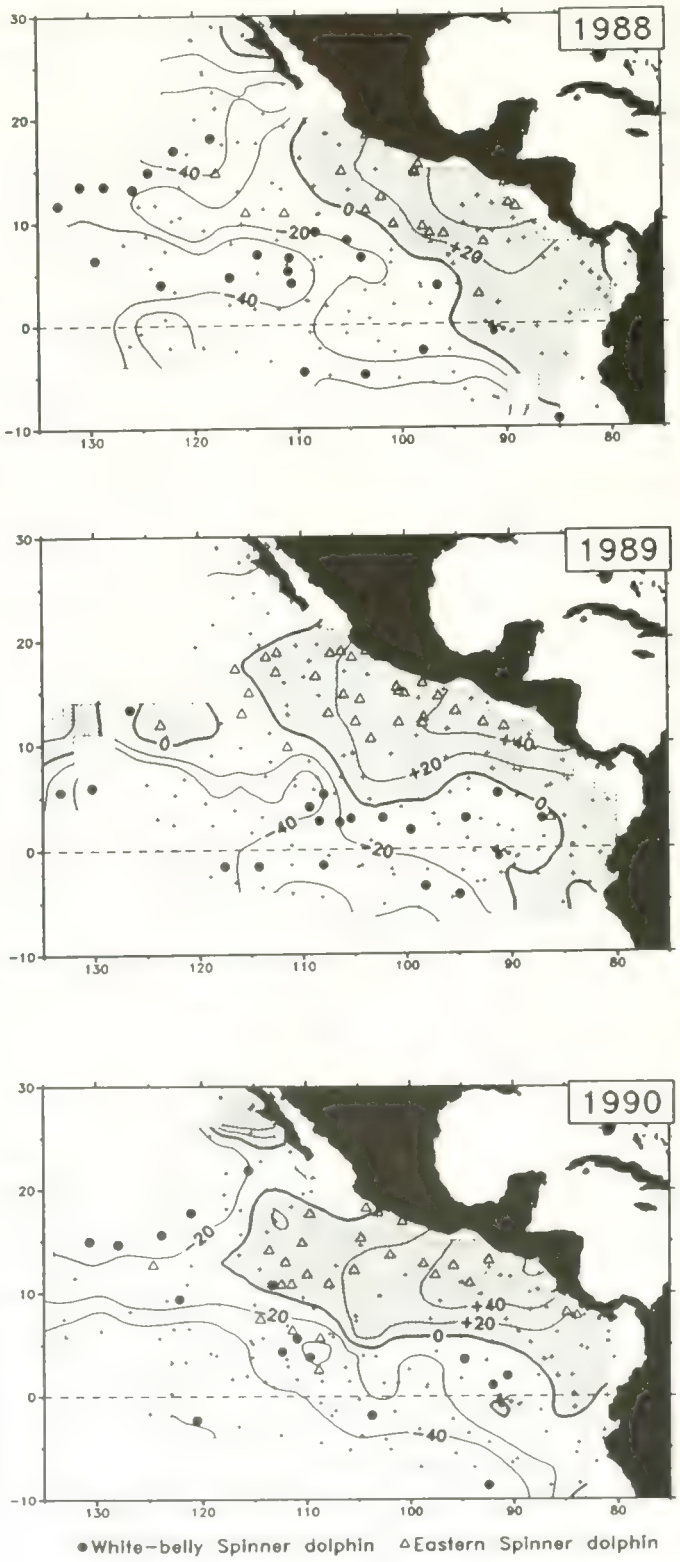

Figure 7 (Continued)

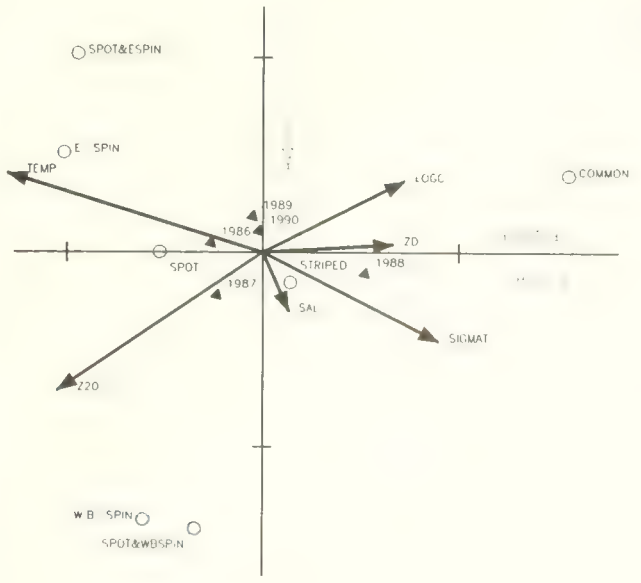

Figure 8

Ordination biplot from canonical correspondence analysis of seven dolphin school types in relation to six oceanographic variables (see Fig. 5 for definitions), with the five sampled years as categories. Mean values for each year are represented by triangles, YEAR 1 = 1986, YEAR 2 = 1987, etc.

Literature cited

Anganuzzi, A. A., and S. T. Buckland.
1989. Reducing bias in trends in dolphin abundance, estimated from tuna vessel data. Rep. Int. Whal. Comm. 39: 323–334.

Anganuzzi, A. A., S. T. Buckland, and K. L. Cattanach.
1991. Relative abundance of dolphins associated with tuna in the eastern tropical Pacific, estimated from tuna vessel sightings for 1988 and 1989. Rep. Int. Whal. Comm. 42:497–506.

Au, D.W. K., and W. L. Perryman.
1985. Dolphin habitats in the eastern tropical Pacific. Fish. Bull. 83:623–643.

Blackburn, M., R. M. Laurs, R. S. Owen, and B. Zeitschel.
1970. Seasonal and areal changes in standing stocks of phytoplankton, zooplankton and micronekton in the eastern tropical Pacific. Mar. Biol. 7:14–31.

Carr, A.
1987. New perspectives on the pelagic stage of sea turtle development. Conserv. Biol. 1(2):103–121.

Chavez, F. P., and R. T. Barber.
1987. An estimate of new production in the equatorial Pacific. Deep-Sea Res. 24:1229–1243.

Dizon, A. E., S. O. Southern, and W. F. Perrin.
1991. Molecular analysis of mtDNA types in exploited populations of spinner dolphins (*Stenella longirostris*). *In* R. Hoelzel (ed.), Genetic ecology of whales and dolphins. Rep. Int. Whal. Comm., Spec. Issue 13:183–202.

Dizon, A. E., W. F. Perrin, and P. A. Akin.
In press. Stocks of dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific: a phylogeographic classification. NOAA Technical Rep. NMFS.

Donguy, J. R., and G. Meyers.
1987. Observed and modelled topography of the 20°C isotherm in the tropical Pacific. Oceanologica Acta 10:41–48.

Enfield, D. B.
1989. El Niño, past and present. Rev. Geophys. 27:159–187.

Evans, W. E.
1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* Linnaeus in the northeastern Pacific. Ph.D. thesis, Univ. Calif. Los Angeles.

Fiedler, P. C.
1992. Seasonal climatologies and variability of eastern tropical Pacific surface waters. NOAA Tech. Rep. NMFS 109, 65 p.

Fiedler, P. C., and S. B. Reilly.
1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. II: Effects on abundances estimated from tuna vessel sightings, 1975–1990. Fish. Bull. 92:451–463.

Fiedler, P. C., L. J. Lierheimer, S. B. Reilly, S. N. Sexton, R. S. Holt, and D. P. DeMaster.
1990. Atlas of eastern tropical Pacific oceanographic variability and cetacean sightings, 1986–1989. NOAA Tech. Memo. NMFS-SWFSC-144.

Fiedler, P. C., F. P. Chavez, D. W. Behringer, and S. B. Reilly.
1992. Physical and biological effects of Los Niños in the eastern tropical Pacific. Deep-Sea Res. 39(2):199–219.

Gauch, H. G., Jr.
1982. Multivariate analysis in community ecology. Cambridge Univ. Press.

Gerrodette, T., and P. R. Wade.
1991. Monitoring trends in dolphin abundance in the eastern tropical Pacific: analyses of 1989 data. Rep. Int. Whal. Comm. 41:511–515.

Haury, L. R., J. A. McGowan, and P. H. Wiebe.
1978. Patterns and processes in the time-space scales of plankton distributions. *In* J. H. Steele (ed.), Spatial pattern in plankton communities. Plenum Press, New York.

Holt, R. S.
1987. Estimating density of dolphin schools in the eastern tropical Pacific Ocean by line transect methods. Fish. Bull. 85:419–434.

Holt, R .S., and S. N. Sexton.
1990. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1986 data, the first year. Fish. Bull. 88: 105–111.

Holt, R. S., T. Gerrodette, and J. B. Cologne.
1987. Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific. Fish. Bull. 85:435–446.

Hope, A. C. A.
1968. A simplified Monte Carlo significance test procedure. R. Statist. Soc. J. Ser. B 30(3):582-598.

King, F. D.
1986. The dependence of primary production in the mixed layer of the eastern tropical Pacific on the vertical transport of nitrate. Deep-Sea Res. 33(6):733–754.

Kirschvink, J. L., A. E. Dizon, and J. A. Westphal.
1986. Evidence from strandings for geomagnetic sensitivity in cetaceans. J. Exp. Biol. 120:1–24.

Klinowska, M.
1985. Cetacean stranding sites relate to geomagnetic topography. Aquatic Mammals 1:27–32.

Kousky, V. E., and A. Leetmaa.
1989. The 1986–87 Pacific warm episode: evolution of oceanic and atmospheric anomaly fields. J. Clim. 2:254–267.

Leatherwood, S., R. R. Reeves, W. F. Perrin, and W. E. Evans.
1982. Whales, dolphins and porpoises of the eastern North Pacific and adjacent waters, a guide to their identification. NOAA Tech. Rep. NMFS Circ. 444.

Leetmaa, A.
1990. The interplay of El Niño and La Niña. Oceanus 32:30–34.

McCreary, J. P., H. S. Lee, and B. B. Enfield.
1989. The response of the coastal ocean to strong offshore winds: with application to circulations in the Gulfs of Tehuantepec and Papagayo. J. Mar. Res. 47:81–109.

Perrin, W. F.
1969. Using porpoise to catch tuna. Wld. Fish. 18(6):42–45.
1975. Distribution and differentiation of populations of dolphin of the genus *Stenella* in the eastern tropical Pacific. J. Fish. Res. Board. Can. 32:1059–1067.
1990. Subspecies of *Stenella longirostris* (Mammalia: Cetacea: Delphinidae). Proc. Biol. Soc. Wash. 103(2):453–463.

Perrin, W. F., M. D. Scott, G. J. Walker, F. M. Ralston, and D. W. K. Au.
1983. Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific. NOAA Tech. Memo. NMFS-SWFC-38, 65 p.

Perrin, W. F., M. D. Scott, G. J. Walker, and V. Cass.
1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific. NOAA Tech. Rep. NMFS 28, 28 p.

Pickard, G. L., and W. J. Emery.
1982. Descriptive physical oceanography, 4th (SI) enlarged ed. Pergamon Press, Oxford, 249 p.

Pimentel, R. A.
1979. Morphometrics. The multivariate analysis of biological data. Kendall/Hunt Publ. Co., Dubuque, Iowa, 276 p.

Reilly, S. B.
1990. Seasonal changes in distribution and habitat differences among dolphins in the eastern tropical Pacific. Mar. Ecol. Prog. Ser. 66(1–2):1–11.

Smith, T. D.
1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fish. Bull. 81:1–13.

Ter Braak, C. J. F.
1985. Correspondence analysis of incidence and abundance data: properties in terms of a unimodal response model. Biometrics 41:859–873.
1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67(5):1167–1179.
1988. CANOCO— a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Tech. Rep. LWA-88-02, Groep Landbouwwiskunde, Postbus 100,6700 AC Wageningen, The Netherlands.

Townsend, C. H.
1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica Sci. Contrib. N.Y. Zool. Soc. 19(1):1–50.

Tsuchiya, M.
1974. Variation of surface geostrophic flow in the eastern intertropical Pacific Ocean. Fish. Bull. 72(4):1075–1086.

Whittaker, R. H., S. A. Levin, and R. B. Root.
1973. Niche, habitat and ecotope. Am. Nat. 107:321–338.

Wyrtki, K.
1964. Upwelling in the Costa Rica Dome. Fish. Bull. 63:355–372.
1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Ann. Rev. 4:33–68.
1967. Circulation and water masses in the eastern equatorial Pacific Ocean. Int. J. Oceanol. Limnol. 1:117–147.

Young, T. L., and M. L.Van Woert.
1987. PLOT88 software library. Plotworks, Inc., La Jolla, CA.

Interannual variability of dolphin habitats in the eastern tropical Pacific. II: Effects on abundances estimated from tuna vessel sightings, 1975–1990

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Abstract.—The results of a canonical correspondence analysis (CCA) of data from research vessel surveys of the eastern tropical Pacific were applied to time series of estimated dolphin abundances from tuna vessel sightings. The research vessel survey data consisted of daily dolphin school sightings and concurrent environmental variables for August–November of 1986 through 1990. Seasonal fields of habitat quality for 1975-90 were calculated from historical bathythermograph data by using the CCA ordination results. For spotted (*Stenella attenuata*) and eastern spinner (*S. longirostris orientalis*) dolphins, annual abundance estimates or interannual changes in those estimates are significantly correlated with habitat quality. This effect is at least partly due to expansion of high quality habitat beyond the geographic ranges assumed for the abundance estimate. We discuss ways that environmental data could be used to reduce error in dolphin abundance estimates.

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The eastern tropical Pacific Ocean (ETP) supports a diverse and abundant cetacean fauna. By the late 1960s, it had become clear that large numbers of dolphins were being killed in tuna purse seine operations (Perrin, 1969). The dolphin species affected by the tuna fishery, known as "target species," are spotted dolphin (*Stenella attenuata*), the "whitebelly" form and "eastern" subspecies of spinner dolphin (*S. longirostris* and *S. l. orientalis*, Perrin, 1990), common dolphin (*Delphinus delphis*), and striped dolphin (*S. coeruleoalba*). In 1973, the U.S. government initiated a formal program to place observers on purse seiners to monitor dolphin mortality (Smith, 1983). In 1975, the Inter-American Tropical Tuna Commission began putting observers on the international fleet. The tuna vessel observer data from these programs includes sightings of cetaceans, as well as mortality data and biological samples from incidental catches.

Time series of target species abundance have been estimated from tuna vessel observer data (Buckland et al., 1992). These are yearly estimates of stocks of spotted, spinner, and common dolphins within nominal stock boundaries known as the Status of Porpoise Stocks or SOPS boundaries.[1] Buckland et al. (1992) analyzed smoothed time series of these estimates and detected significant trends for some stocks.

Time series of dolphin abundance estimates are subject to considerable sampling error plus the effects of environmental variability on abundance and distribution. The effect of environmental factors on abundance estimates must be quantified before such a time series can be properly interpreted in terms of abundance changes or trends. This paper analyzes relationships between abundance estimates from tuna vessel observer data and environmental variability. Since little or no environmental data are collected on these ships, we base our analysis on species-environment relationships derived from research vessel data (Reilly and Fiedler, 1994).

National Marine Fisheries Service research vessels have surveyed the ETP several times since 1974 to collect data for abundance estimates and supplement the tuna vessel observer data (Holt et al., 1987). The most extensive research vessel observer data were collected

[1] Au, D. W. K., W. L. Perryman, and W. F. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. NOAA/SWFC Admin. Rep. No. LJ-79-43, 59 p.

for the Monitoring of Porpoise Stocks (MOPS) program during August-November in 1986 through 1990 (Wade and Gerrodette, 1992). The MOPS surveys were designed to cover the SOPS spotted, spinner, and common dolphin stock boundaries. Reilly and Fiedler (1994) showed that sighting rates of dolphin species or school types on the MOPS surveys were related to concurrently measured environmental variables. We used a robust and efficient multivariate technique, canonical correspondence analysis, to examine relations between spatial distributions of dolphin species and environmental variables.

Canonical correspondence analysis (CCA) was developed to relate community composition to known variation in the environment. It is a form of direct gradient analysis that directly estimates ordination axes as linear combinations of observed environmental variables (Ter Braak, 1986). The advantages of CCA for multivariate species-environment analyses and details of the method are discussed by Reilly and Fiedler (1994). CCA estimates unimodal (Gaussian) responses of species along the ordination axes. In general, the response is observed abundance or probability of occurrence. We assume that a species response (abundance observed at a site in time and space) reflects the suitability of environmental conditions at that site relative to the species' optimal habitat or niche. This suitability, or habitat quality, is defined by the response distribution along the axes. An observed response will also include error caused by behavioral responses to the environment that affect the detectability of schools.

In this paper, we analyze relations between abundance estimates and habitat quality. It must be stated at the outset that in a 15-year record of populations with growth rates of only ~0.02 yr^{-1} (Reilly and Barlow, 1986), we are able to detect short-term environmental effects on sampling but not long-term effects on population size. Nevertheless, we demonstrate that some of the interannual variability in estimated abundances of ETP dolphins can be explained by environmental factors.

Methods

We used archived bathythermograph data to quantify variability of surface temperature, thermocline depth, and thermocline thickness in the MOPS study area since 1975. These variables were shown to be important in explaining variations in encounter rates in the MOPS surveys (Reilly and Fiedler, 1994). Other important variables (salinity and chlorophyll concentration) have not been routinely observed with sufficient frequency to be used in this historical analysis. Seasonal fields (gridded values) of surface temperature, thermocline depth, and thermocline thickness for the period 1975–90 were derived from a bathythermograph data base originally described by Fiedler (1992) and augmented with data from other sources for this study (Table 1). Thermocline depth is defined as the depth of the 20°C isotherm. Thermocline thickness is defined as the difference in depth between the 20°C and 15°C isotherms.

Data were objectively gridded by seasons (December–February, March–May, June–August, September–November from 1975 through 1990) on a 2-degree latitude-longitude grid from lat. 20°S to 30°N latitude and from the coast out to long. 160°W. Decorrelation scales, the distances required for a substantial change in surface temperature or thermocline depth, have been estimated as 3 degrees latitude and 15 degrees longitude in this region (Sprintall and Meyers, 1991). At each grid point, means of at least 20 observations within up to 4 degrees latitude and 20 degrees longitude were calculated. The observations were weighted by the re-

Table 1

Numbers of bathythermograph profiles, after screening for errors and replicates, used to define habitat quality in yearly seasonal grids (1975–90) and in climatologies (1960–91). **NODC** = NOAA/NESDIS/National Oceanographic Data Center CD-ROM NODC-03: Global Ocean Temperature and Salinity Profiles, vol. 2, Pacific Ocean; **MOODS** = Navy Master Oceanographic Observations Data Set, including non-NODC observations through 1983 obtained from the Naval Oceanographic Office through NODC and 1985–90 observations obtained from Steve Pazan, Scripps Institution of Oceanography; **SOP** = French-American ship-of-opportunity observations obtained from NOAA/ERL/Pacific Marine Environmental Laboratory (Kessler, 1990); **FSFRL** = Japanese Far Seas Fisheries Research Laboratory MBT data obtained from PMEL and from NOS/Ocean Applications Branch (these data will be added to the NODC data set in the near future).

	1975–90	1960–91
NODC	61,486	127,365
MOODS	10,741	15,077
SOP	2,859	11,305
FSFRL	2,350	4,744
Total	77,436	158,491

ciprocal of the distance from the grid point. The range of observations around a grid point was increased in increments of 0.4 degrees latitude and 2 degrees longitude to obtain a minimum sample size of 20 for each grid point. Thus, local grid resolution decreases in data-poor regions, generally south of the equator where the maximum distance required was up to 20 degrees longitude. Within the MOPS area, sufficient observations were available within 2 degrees latitude and 10 degrees longitude of 71% of the gridpoints, and within 4 degrees latitude and 20 degrees longitude of 95% of the gridpoints. We converted observations to anomalies (deviations from the seasonal mean) before gridding to reduce the spatial variability of the observations. This minimized bias caused by interpolation over or extrapolation into large data gaps.

Relationships among abundances of dolphin species and environmental variables were analyzed by using CCA as described in Reilly and Fiedler (1994). Encounter rate, equal to number of schools sighted per unit of sighting effort (trackline distance), was used as a measure of relative abundance. The final abundance estimate also depends on school size and effective track width. However, Reilly and Fiedler (1994) found that weighting encounter rates by estimated school size in the CCA produced essentially the same species-environment patterns. Therefore, schools of all sizes occupied approximately the same habitats and school size variability within these habitats was not related to the environmental variables included in the analysis.

CCA was performed on MOPS sightings and environmental data as in Reilly and Fiedler (1994), except that mixed schools of spotted and spinner dolphins were counted as schools of both species rather than as an additional "species." Also, we used Hill's symmetric scaling of species and site scores (S=–3 in our implementation of CANOCO[2]). This alternative scaling of the ordination had no qualitative effect on species-environment patterns but seemed to give more reasonable results at the edges of the study area when scores were combined to quantify species habitat distributions.

Habitat quality for species i (H_i) at a gridpoint was calculated from the Gaussian responses fit to the two dominant canonical axes by CCA. The response to each environmental axis was calculated as a normal probability density function:

$$H_{ij} = t_{ij}^{-1} \exp\left(-0.5 * \left(\left(x_j - u_{ij}\right)/t_{ij}\right)^2\right),$$

where,

x_j = the site (gridpoint) score on environmental axis j,

u_{ij} = the species i score (optimum) on axis j,

t_{ij} = the tolerance (standard deviation) of species i on axis j.

Species scores and tolerances (u_{ij} and t_{ij}) were output by CANOCO as part of the CCA. Site scores (x_j) were calculated as linear combinations, defined by the output canonical axis coefficients, of normalized and gridded environmental observations. Habitat quality, H_i, was then calculated as the geometric mean of H_{ij}'s; each H_{ij} was scaled so that the mean value is 1.0 during 1975–90. Thus, H_i is equal to the abundance expected at a site, based on local environmental conditions, divided by the mean abundance in the study area during 1975–90.

Point estimates of annual abundance were provided by Anganuzzi[3] for pooled stocks: spotted dolphins include northern and southern offshore spotted dolphins, whitebelly spinner dolphins include northern and southern whitebelly spinner dolphins, and common dolphins include northern, central, and southern common dolphins. No estimates were made for striped dolphins, which were rarely set on by tuna vessels.

Results

The species-environment biplot (Fig. 1) summarizes the results of the CCA of five species and three environmental variables observed during 1986–90 MOPS research surveys. The eigenvalues of the three canonical axes were 0.296, 0.074, and 0.001. The first two axes explained 99.7% of the species-environment variance accounted for by all three axes. Therefore, the third axis was not used. The first two axes explained 20.5% of the total variance of species encounter rates (Table 2).

Positive scores on canonical axis 1 indicate cool surface temperature and a shallow, weak thermocline (Table 3). These are characteristics of the productive "cool upwelling" habitat that we identified with the first axis in the complete CCA (seven species and six environmental variables, Reilly and Fiedler, 1994). This habitat is found in the equatorial and eastern boundary current (Peru and Cali-

[2] Ter Braak, C. J. F. (1988). CANOCO—a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Tech. Rept. LWA-88-02, Groep Landbouwwiskunde, Postbus 100, 6700 AC Wageningen, The Netherlands.

[3] Anganuzzi, A. Inter-American Tropical Tuna Commission, 8604 La Jolla Shores Drive, La Jolla, CA 92038. Pers. commun. December 1991.

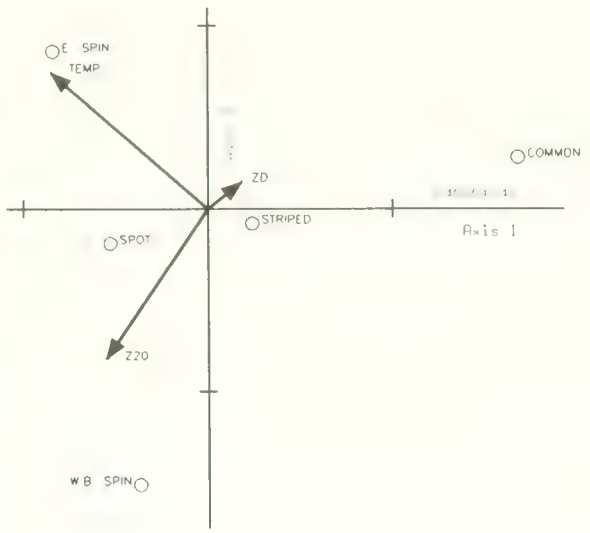

Figure 1

Ordination biplot of first two canonical axes from CCA of species-environment data from 1986–90 MOPS surveys of the ETP. Points represent species scores (optima) and vectors represent the regression relationships of environmental variables with the canonical axes. TEMP = surface temperature, Z20 = thermocline depth, ZD = thermocline thickness. SPOT = spotted dolphin (*Stenella attenuata*), COMMON = common dolphin (*Delphinus delphis*), E. SPIN = eastern spinner dolphin (*S. longirostris orientalis*), W. B. SPIN = whitebelly spinner dolphin (*S. longirostris*), STRIPED = striped dolphin (*S. coeruleoalba*).

Table 2

Fractions of individual and total species variances explained by canonical correspondence analysis (CCA). AX1 = canonical axis 1, AX2 = canonical axis 2. Dolphin species: spotted = *Stenella attenuata*, common = *Delphinus delphis*, eastern spinner = *S. longirostris orientalis*, whitebelly spinner = *S. longirostris*, striped = *S. coeruleoalba*.

	AX1	AX2	AX1+AX2
Spotted	0.191	0.000	0.191
Common	0.321	0.004	0.325
Eastern spinner	0.169	0.089	0.258
Whitebelly spinner	0.014	0.118	0.132
Striped	0.037	0.002	0.039
Total	0.164	0.041	0.205

fornia Currents) waters of the ETP and is also present seasonally in the region of the Costa Rica Dome at 10°N, 90°W (Fiedler, 1992). Positive scores on canonical axis 2 indicate warm surface temperature and a shallow thermocline (Table 3). These are characteristics of the "coastal tropical" habitat of Reilly and Fiedler (1994). This habitat is centered in the warmest tropical surface water of the ETP, along the coast of Mexico south of Baja California.

Species responses along the canonical axes (Fig. 2) showed some separation of species habitats, as in the complete CCA (Reilly and Fiedler, 1994). Axis 1 separated common dolphins from spotted and spinner dolphins, while axis 2 separated eastern and whitebelly spinner dolphins. The means (optima, Table 4) of a species distribution on the two canonical axes in Figure 2 are equal to the species scores plotted in the ordination biplot (Fig. 1).

The validity of the species/environment relationships calculated by CCA was confirmed in three ways. First, distributions of climatological H, derived from the CCA results and climatological values of environmental variables at each gridpoint in the MOPS area (Fiedler, 1992), were consistent with stock ranges indicated by the SOPS population boundaries, with the exception of whitebelly spinner dolphins (Fig. 3). Second, the distributions were similar to patterns in maps of tuna and research vessel sighting records (Perrin et al., 1985), although such maps can give only a rough indication of habitat distribution because the sighting or collection frequencies are not standardized by effort. Third, the distributions of H calculated for climatological September–November environmental conditions were significantly correlated with gridded fields of mean (August–November, 1986–90) MOPS encounter rates as follows: spotted dolphin $r = 0.52$, common dolphin $r = 0.45$, eastern spinner dolphin $r = 0.65$, whitebelly spinner dolphin $r = 0.36$, striped dolphin $r = 0.41$ ($P<0.01$ for all relationships).

Table 3

Regression/canonical coefficients for standardized environmental variables on two environmental axes (AX1 and AX2). TEMP = surface temperature, Z20 = thermocline (20°C isotherm) depth, ZD = thermocline thickness (difference between 20°C and 15°C isotherm depths).

	TEMP	Z20	ZD
AX1	−0.501	−0.326	+0.111
AX2	+0.439	−0.486	+0.088

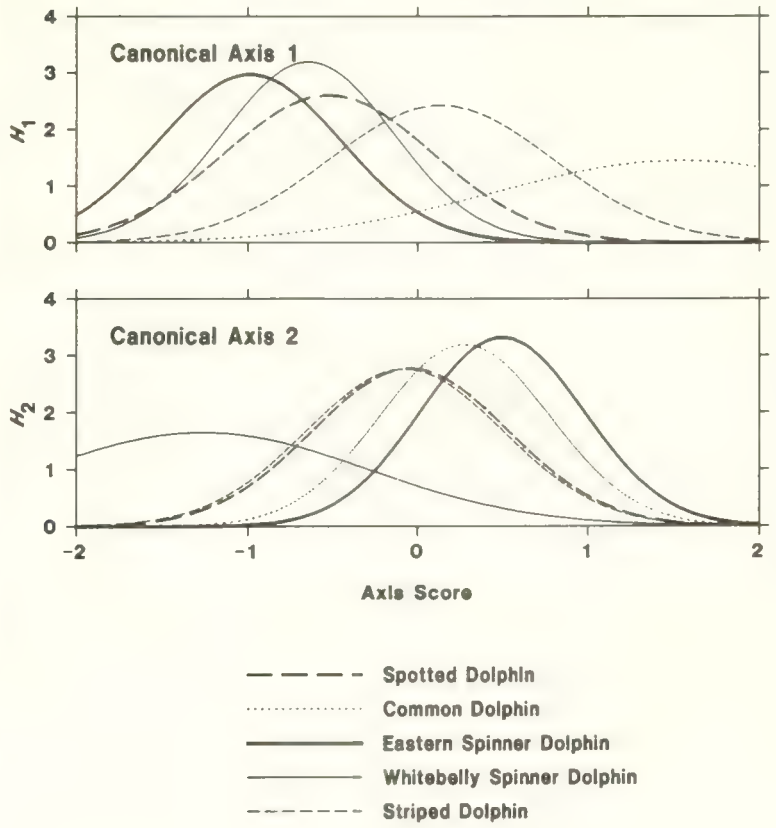

Figure 2

CCA-derived Gaussian distributions of dolphin species habitat quality, H (from MOPS 1986–90 encounter rates), along the first two canonical axes. The values are scaled so that the mean of H_{ij} is 1.0 over a range of ±2 units (standard deviations) on the canonical axis. Spotted dolphin = *Stenella attenuata*, common dolphin = *Delphinus delphis*, eastern spinner dolphin = *S. longirostris orientalis*, whitebelly spinner dolphin = *S. longirostris*, striped dolphin = *S. coeruleoalba*.

Spotted dolphin habitat was centered south and southwest of the southern coast of Mexico to about 3°N (Fig. 3). This corresponds to the warm, tropical surface water mass of Wyrtki (1966, see Fig. 1 in Reilly and Fiedler, 1994). The Costa Rica Dome (10°N, 90°W) was a notable gap in favorable spotted dolphin habitat.

Eastern spinner dolphins were even more closely associated with warm tropical surface water. Highest values of H for this stock were found off southern Mexico, in the center of the "coastal tropical" habitat defined by canonical axis 1 (Reilly and Fiedler, 1994). Whitebelly spinner dolphins were associated with subtropical surface water (Wyrtki, 1966) to the northwest and southwest of the tropical surface water in the core of the MOPS area.

Table 4

Dolphin species scores (standardized) ±tolerances on the first two canonical axes from canonical correspondence analysis (CCA). Dolphin species: spotted = *Stenella attenuata*, common = *Delphinus delphis*, eastern spinner = *S. longirostris orientalis*, whitebelly spinner = *S. longirostris*, striped = *S. coeruleoalba*.

	AX1	AX2
Spotted	−0.53 ± 0.57	0.19 ± 0.54
Common	1.68 ± 1.16	0.28 ± 0.48
Eastern spinner	−0.84 ± 0.49	0.86 ± 0.71
Whitebelly spinner	−0.37 ± 0.55	−1.51 ± 1.19
Striped	0.24 ± 0.69	−0.08 ± 0.55

Common dolphin habitat was centered in cool, upwelling-modified water in three regions: off Baja California, along 10°N with a maximum at the Costa Rica Dome, and in the equatorial surface water mass of Wyrtki (1966). These three habitat centers are occupied by the northern, central, and southern stocks of common dolphins (Perrin et al., 1985). The offshore H maximum along 10°N at 120–130°W does not correspond to high encounter rates in the MOPS data, but reflects a shoaling of the countercurrent thermocline ridge at that location (Fiedler, 1992).

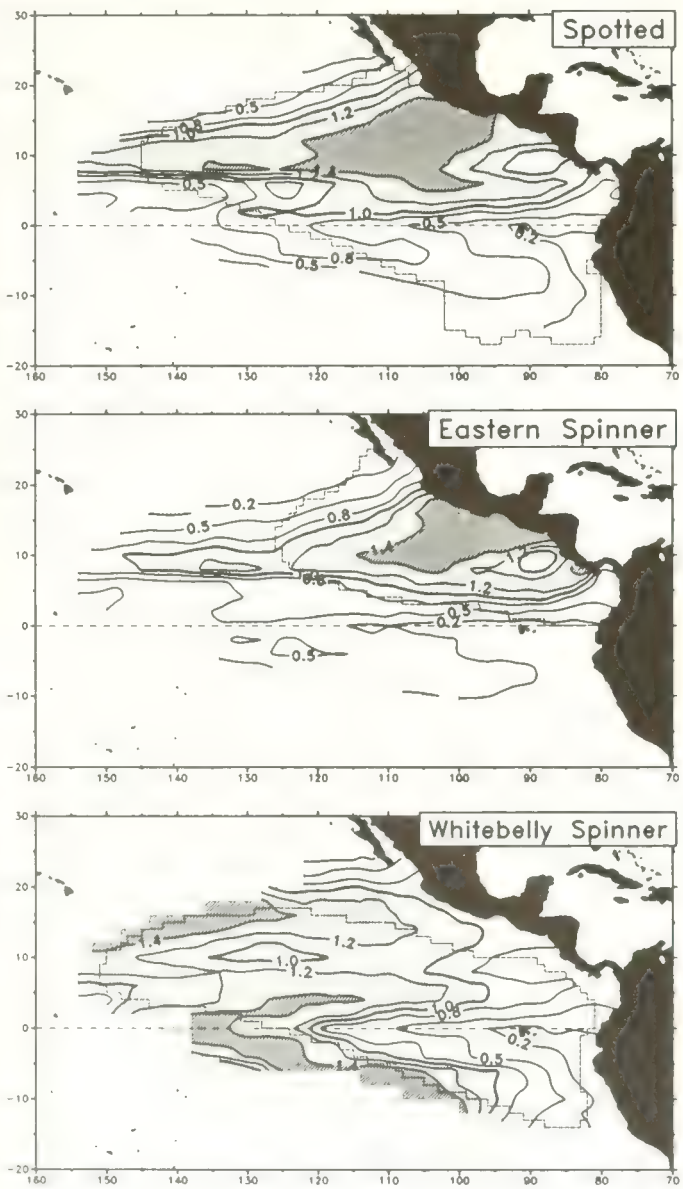

Figure 3

Mean habitat quality (H) for spotted (*Stenella attenuata*), eastern spinner (*S. longirostris orientalis*), whitebelly spinner (*S. longirostris*), common (*Delphinus delphis*), and striped (*S. coeruleoalba*) dolphins. H was calculated from climatological fields of surface temperature, thermocline depth, and thermocline thickness in the MOPS area. Heavy dashed lines delimit SOPS population areas used by Anganuzzi and Buckland (1989) and Anganuzzi et al. (1991) or, for striped dolphins, as defined by Au et al. (Footnote 1.)

Striped dolphins are the most widespread and abundant of the target species. The highest H values tended to be in regions between or offshore of the centers of spotted/eastern spinner dolphin habitat in tropical surface water near the coast of southern Mexico and northern, central, and southern common dolphin habitats off Baja California, near the Costa Rica Dome, and in equatorial water (see also Reilly, 1990).

Both seasonal and interannual variability were evident in time series of mean seasonal habitat quality, H (Fig. 4). The strongest interannual signal for all species can be attributed to the El Niño events of 1982–83 and 1986–87. During both events, H increased for spotted and spinner dolphins and decreased for common and striped dolphins. Seasonal variability, indicated by the deviations of the seasonal from the smoothed H values, was low for species with large geographic ranges (e.g. striped dolphin) and high for species with more restricted ranges (e.g. eastern spinner dolphin). Seasonal variability of H was as great as interannual variability for eastern spinner dolphins.

Annual dolphin abundance estimates, N_t, or interannnual change in abundance estimates, N_t–N_{t-1}, were related to changes in the environment, H, for spotted and eastern spinner dolphins. Annual spotted dolphin abundance was not significantly correlated with H, but interannual change in abundance was negatively correlated with H (Fig. 5, r=–0.65, P=0.01). Calculating year-to-year changes in abundance eliminates multi-year trends in the time series. Buckland et al. (1992) found significant trends in estimated spotted dolphin abundance which might complicate the relation between annual N and H values. An increase in H for spotted dolphins indicates an expansion of favorable habitat to the south of the SOPS population boundary west of 100°W (Fig. 6A).

Annual eastern spinner dolphin abundance was negatively correlated with H (r=–0.49, P=0.05). An increase in H for eastern spinner dolphins indicates an expansion of favorable habitat to the west and south of the SOPS population boundary (Fig. 6B).

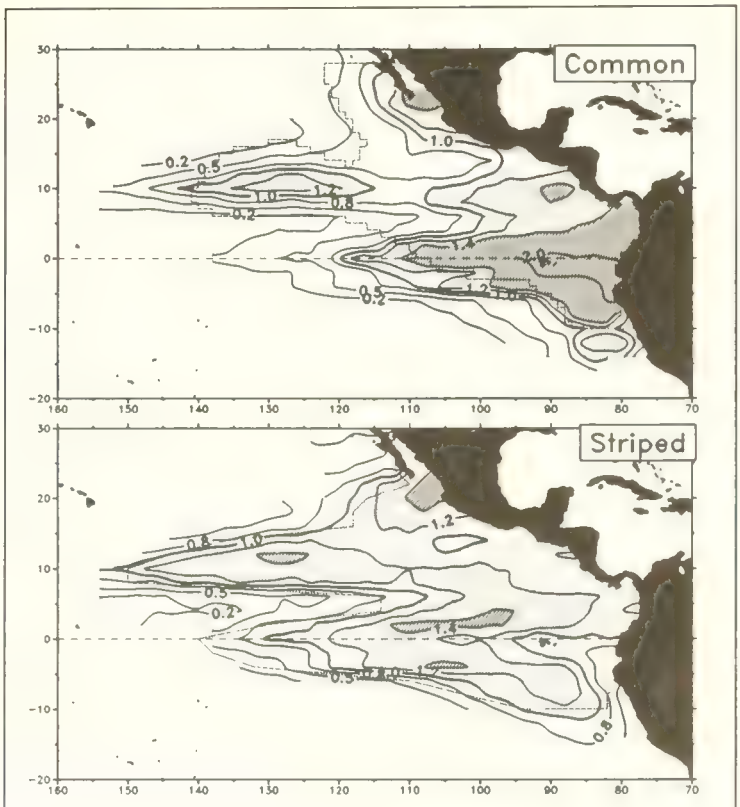

Figure 3 (Continued)

Common and whitebelly spinner dolphins did not show significant linear relationships between N and H (Fig. 7). For all four species, log-transformation of the abundance estimates or lagging N_t by up to four seasons did not change the significance levels of the linear relationships. However, common dolphin abundance appeared to be maximum at H near 1.0 and to decrease at lower or higher H values, except in 1983. Scatterplots of N_t vs. H_t for spotted and whitebelly spinner dolphins suggest similar nonlinear relationships. For common dolphins at low values of H, as in early 1983, very little high-quality or favorable habitat was available in the ETP (Fig. 6C). The only favorable habitat with $H>1$ was in equatorial water west of the Galapagos. Half of this favorable habitat was outside the SOPS boundary. At high values of H, as in early 1985, favorable habitat for the central and southern stocks (along 10°N and the equator, respectively) expanded. Favorable habitat along the equator extended beyond the SOPS boundary. At the same time, favorable habitat for the more abundant northern stock, off Baja California, was reduced.

Discussion

Estimated abundances of spotted and eastern spinner dolphins in the eastern tropical Pacific were correlated with changes in the environment, as described by the CCA-derived habitat quality index H. The time scale of the changes and the patterns of favorable habitat relative to nominal population boundaries (Fig. 6) suggest that the correlations resulted from a sampling effect, rather than a population effect. Thus, we have explained biases in annual population estimates that result in apparent population changes. For example, Anganuzzi and Buckland (1989) suggested that their low 1983 abundance estimate for spotted dolphins might be explained by dispersal of local concentrations of schools during the strong El Niño. Our results showed that spotted dolphin schools may have moved outside the nominal species range when the "coastal tropical" habitat expanded into equatorial water west of 100°W during this unusual event. Similarly, estimated eastern spinner dolphin abundance decreased slightly with increasing H because

of the dispersal of schools outside the nominal range used in calculating the abundance estimate. The center of distribution of spotted and eastern spinner dolphins is the warm tropical surface water in the core of the ETP. Therefore, the apparent responses of the two populations to environmental variability are similar.

The different effects of environmental variability on the habitats of the three stocks of common dolphins appear to complicate the response of the population as a whole. Data collected during surveys of the central and northern stocks of common dolphins in fall 1992 and 1993, respectively, will allow us to quantify stock-specific habitats and, perhaps, responses to environmental variability. We detected no effect of environmental variability on the abundance estimates of whitebelly spinner dolphins, but the CCA results inadequately define the geographical

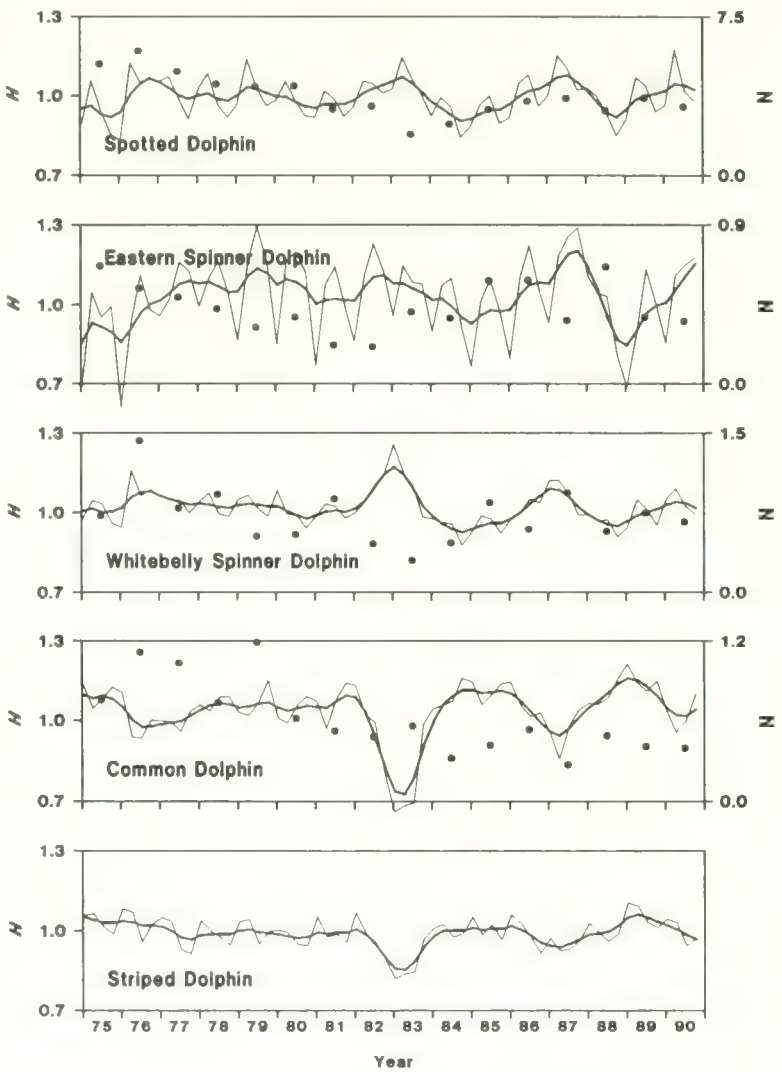

Figure 4

Mean SOPS area habitat quality (H) for five dolphin species: seasonal values (thin line) and smoothed values (five-season running mean, thick line). Dots are point estimates of species abundance ($N \times 10^{-6}$). Spotted dolphin = *Stenella attenuata*, common dolphin = *Delphinus delphis*, eastern spinner dolphin = *S. longirostris orientalis*, whitebelly spinner dolphin = *S. longirostris*, striped dolphin = *S. coeruleoalba*.

extent of the habitat of this stock (see Fig. 3). The apparent westward extension of the habitat outside the MOPS area is consistent with the recognition of the "whitebelly" form as a hybrid/intergrade between eastern and pantropical subspecies of spinner dolphins (Perrin, 1990). The partial separation of eastern and whitebelly spinner dolphin habitats defined by H is consistent with the management boundary between the two forms proposed by Perrin et al. (1991): eastern spinners north of 10°N and east of 125°W, and whitebelly spinners south of 10°N or west of 125°W.

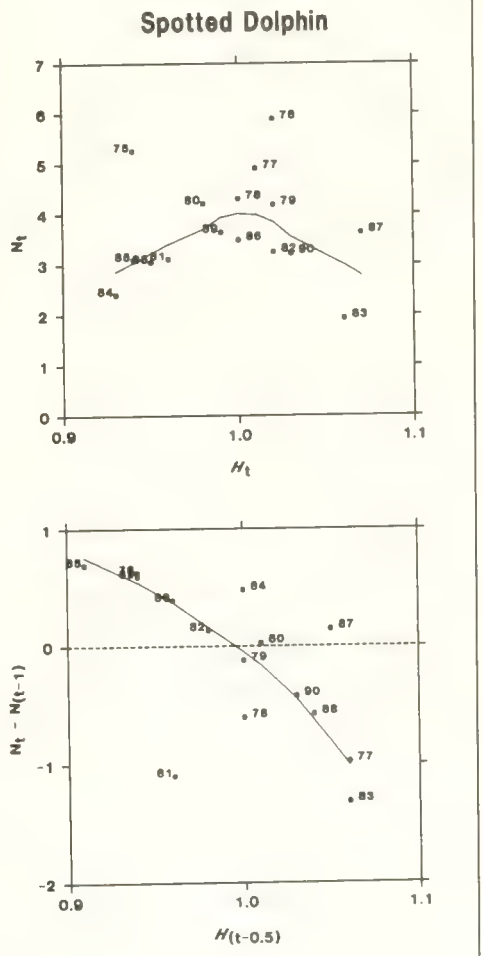

Figure 5

Abundance-environment relationships for spotted dolphins (*Stenella attenuata*) in the MOPS area: (**Top**) Annual abundance estimates ($N_t \times 10^{-6}$) vs. annual mean habitat quality (H_t). (**Bottom**) Interannual change in abundance estimates ($N_t - N_{t-1}$, $\times 10^{-6}$) vs. mean habitat quality from June of year ***t*-1** through May of year ***t*** ($H_{t-0.5}$). Solid line connects lowess-smoothed values (Wilkinson, 1990).

Reilly and Fiedler (1994) suggested that species habitats defined by axis scores from CCA could be used to improve the precision and accuracy of abundance estimates from research vessel surveys. Precision could be increased by post-stratifying the sighting data based on the spatial distribution of axis scores. Bias could be reduced by using axis scores to quantify the amount of habitat available within a survey area. The present results suggest that this approach could be extended by using species habitat distributions incorporating environmental variability along more than one canonical axis. For example, a large area of suitable spotted dolphin habitat existed in equatorial water beyond the SOPS population boundary during 1983, apparently causing a serious underestimate of abundance. Gerrodette et al.[4] suggested similar approaches for using fields of H to adjust abundance estimates from MOPS research vessel surveys.

We utilized the results of a multi-species CCA for this study. While this approach yields useful information about community structure, as in the separation of eastern and whitebelly spinner habitat, it does not retain the maximum amount of information about any single species for management applications. A similar type of analysis for each individual species or stock might explain more of the variability in abundance and improve the quantification of habitat quality defined by Gaussian responses along dominant environmental gradients. In addition, CCA could potentially be used to account for environmental effects on school size and effective trackline width that cause error in dolphin abundance estimates. However, preliminary results of a CCA incorporating school size (Reilly and Fiedler, 1994) showed no meaningful relation between school size and environmental variability. We have only begun to exploit CCA in our work and believe it is a powerful new technique with great potential for quantitative ecological studies of populations of marine mammals and other organisms. For example, environmental variability dominates variations in recruitment of many fish stocks (Longhurst, 1984; Hollowed et al., 1987). Although our time series was not long enough to address population change, this study demonstrates the potential of CCA to detect environmental effects in multi-stock fisheries studies.

[4] Gerrodette, T., P. C. Fiedler, and S. B. Reilly. 1991. Including habitat variability in line transect estimation of abundance and trends. NMFS/SWFSC Admin. Rep. No. LJ-91-37.

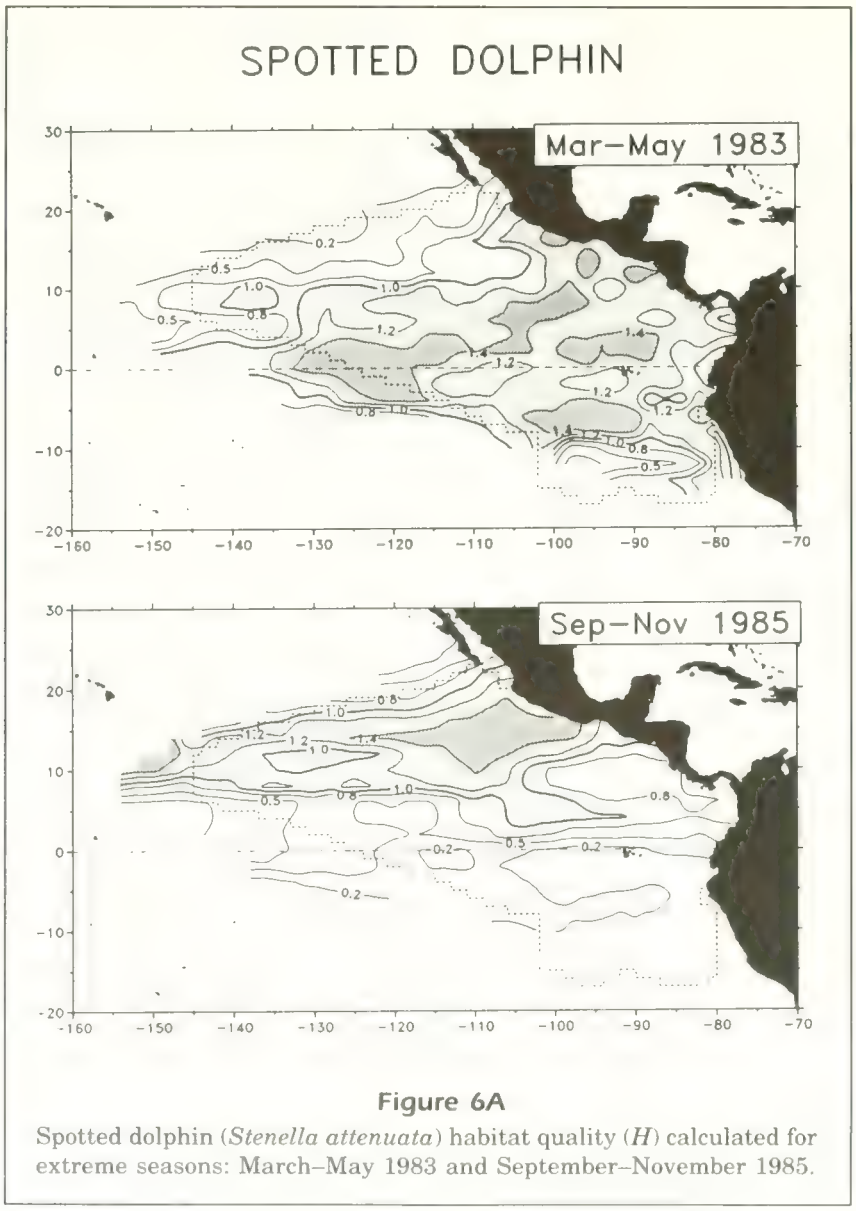

Figure 6A

Spotted dolphin (*Stenella attenuata*) habitat quality (H) calculated for extreme seasons: March–May 1983 and September–November 1985.

Acknowledgments

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Literature cited

Anganuzzi, A. A., and S. T. Buckland.
1989. Reducing bias in trends in dolphin relative abundance, estimated from tuna vessel data. Rep. Int. Whal. Comm. 39:323–334.

Buckland, S. T., K. L. Cattanach, and A. A. Anganuzzi.
1992. Estimating trends in abundance of dolphins associated with tuna in the eastern tropical Pacific Ocean, using sightings data collected on commercial tuna vessels. Fish. Bull. 90:1–12.

Fiedler, P. C.
1992. Seasonal climatologies and variability of eastern tropical Pacific surface waters. Dep. Commer., NOAA Tech. Rep. NMFS 109, 65 p.

Hollowed, A. B., K. M. Bailey, and W. S. Wooster.
1987. Patterns in recruitment of marine fishes in

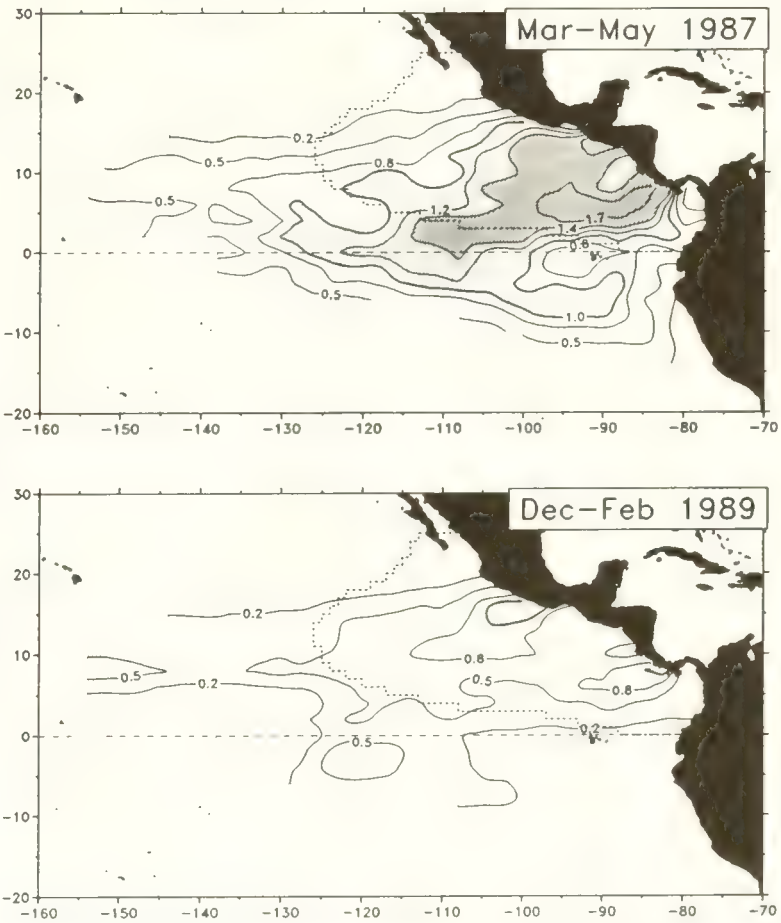

Figure 6B

Eastern spinner dolphin (*Stenella longirostris orientalis*) habitat quality (*H*) calculated for extreme seasons: March–May 1987 and December 1988–February 1989.

the northeast Pacific Ocean. Biol. Oceanogr. 5:99–131.

Holt, R. S., T. Gerrodette, and A. B. Cologne.
1987. Research vessel survey design for monitoring dolphin abundance in the eastern tropical Pacific. Fish. Bull. 85:435–446.

Kessler, W. S.
1990. Observations of long Rossby waves in the northern tropical Pacific. J. Geophys. Res. 95(C4):5183–5217.

Longhurst, A.
1984. Heterogeneity in the ocean - implications for fisheries. Rapp. P.-v. Réun. int. Explor. Mer, 185:268–282.

Perrin, W. F.
1969. Using porpoise to catch tuna. World Fish. 18(6):42–45.
1990. Subspecies of *Stenella longirostris* (Mammalia: Cetacea: Delphinidae). Proc. Biol. Soc. Wash. 103:453–463.

Perrin, W. F., M. D. Scott, G. J. Walker, and V. L. Cass.
1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. Dep. Commer., NOAA Tech. Rep. NMFS 28, 28 p.

Perrin, W. F., P. A. Akin, and J. V. Kashiwada.
1991. Geographic variation in external morphology of the spinner dolphin *Stenella longirostris* in the eastern Pacific and implications for conservation. Fish. Bull. 89:411–428.

Reilly, S. B.
1990. Seasonal changes in distribution and habitat

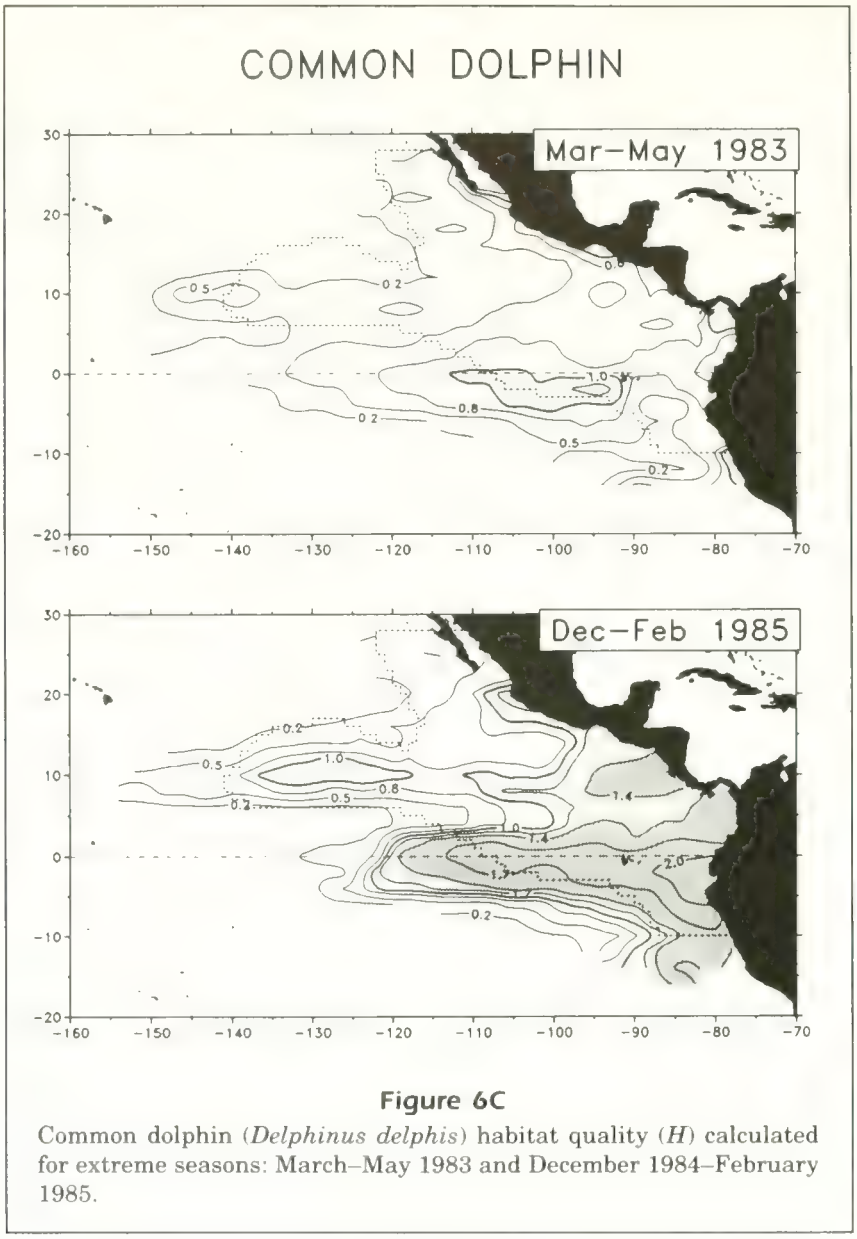

Figure 6C

Common dolphin (*Delphinus delphis*) habitat quality (*H*) calculated for extreme seasons: March–May 1983 and December 1984–February 1985.

differences among dolphins in the eastern tropical Pacific. Mar. Ecol. Prog. Ser. 66:1–11.

Reilly, S. B., and J. Barlow.
1986. Rates of increase in dolphin population size. Fish. Bull. 84:527–533.

Reilly, S. B., and P. C. Fiedler.
1994. Interannual variability of dolphin habitats in the eastern tropical Pacific. I: Research vessel surveys, 1986–1990. Fish. Bull. 92:434–450.

Smith, T. D.
1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fish. Bull. 81:1–13.

Sprintall, J., and G. Meyers.
1991. An optimal XBT sampling network for the eastern Pacific Ocean. J. Geophys. Res. 96(C6): 10,539–10,552.

Ter Braak, C. J. F.
1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.

Wade, P. R., and T. Gerrodette.
1992. Estimates of dolphin abundance in the eastern tropical Pacific: preliminary analysis of five years of data. Rep. Int. Whal. Comm. 42:533–539.

Wilkinson, L.
1990. SYGRAPH: The system for graphics. SYSTAT, Inc., Evanston, IL.

Wyrtki, K.
1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Ann. Rev. 4:33–68.

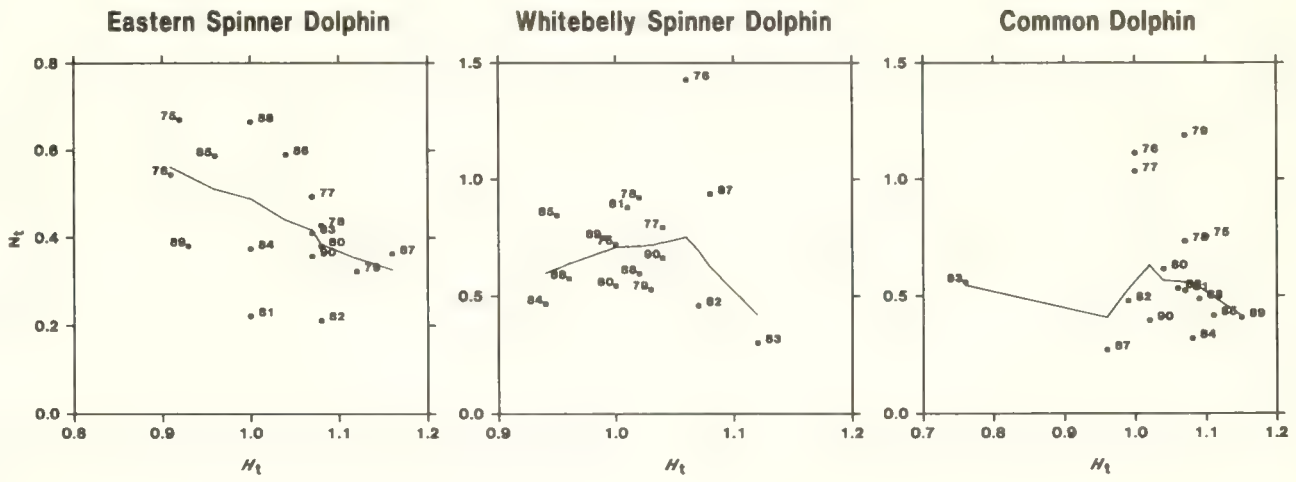

Figure 7

Abundance-environment relations for eastern spinner (*Stenella longirostris orientalis*), whitebelly spinner (*S. longirostris*), and common (*Delphinus delphis*) dolphins in the MOPS area, annual abundance estimates ($N_t \times 10^{-6}$) vs. annual mean habitat quality (H_t). Solid line connects lowess-smoothed values (Wilkinson, 1990).

Annual mass strandings of pelagic red crabs, *Pleuroncodes planipes* (Crustacea: Anomura: Galatheidae), in Bahia Magdalena, Baja California Sur, Mexico

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Pelagic red crabs (or langostilla in Spanish), *Pleuroncodes planipes*, are very abundant galatheid crustaceans off the west coast of Baja California. Some studies suggest that pelagic red crabs are the most abundant species in the micronekton, one of the most important consumers of phytoplankton, and the most common prey item for many marine vertebrates in the area (Boyd, 1962, 1967; Blackburn, 1969; Longhurst et al., 1967; Kato, 1974; Galván, 1988; Balart and Castro[1]).

Although widely used, the common name (pelagic red crab) describes only the planktonic period (about one year) in the life of the species. Larvae, juveniles, and young adults are planktonic. At about 17–20 mm standard carapace length (SCL), they become benthic, making occasional movements to the surface (mostly at night) in a circadian migration (Boyd, 1967). Once the animals reach 32–34 mm SCL, they are fully benthic as are other galatheid species (Boyd, 1967; Aurioles-Gamboa, 1992).

Pelagic red crabs breed from December through April; the peak of the reproductive season is in February (Boyd, 1962; Kato, 1974; Gómez, 1990). Females about 14–15 mm SCL, have been found carrying eggs, but most of the females start to breed when they are about 20 mm SCL (Boyd, 1962; Serrano, 1991).

The benthic population performs seasonal bathymetric movements, at least in the area from lat. 24° to 26° N, in which they disperse during winter and spring to occupy the benthos of the continental shelf (0–200 m depth). After the breeding season, the population moves to deeper waters (100–200 m), and probably invades the continental slope (Aurioles-Gamboa, 1992). Population withdrawal is associated with a rise in bottom temperature above 16°C, and pelagic red crabs remain from June through October in waters 100–200 m deep, where bottom temperature is in the range of 12–16°C (Aurioles-Gamboa, 1992).

One of the notable characteristics in pelagic red crab life history are mass strandings, which have been reported for Bahia Magdalena and the California Coast (Glynn, 1961; Boyd, 1962; Kato, 1974; Stewart et al., 1984). The main difference between strandings in California and Baja California is the frequency of ocurrence. Pelagic red crab beachings in California occur during El Niño events, which enable the population to move northward in warm water currents originating in the south. In contrast, pelagic red crab strandings in Bahia Magdalena are annual, and apparently recur on the same beaches and during the same season of year.

In Bahia Magdalena, pelagic red crabs were observed in the upper 50 cm of water of the surf zone before stranding. Onshore winds and receding tides hasten and intensify stranding (Boyd, 1962). Kato (1974) proposed that the presence of pelagic red crabs near shore is primarily due to winds, waves, and currents.

On 9 May 1991, one of us (D.A-G.) observed a mass stranding of pelagic red crabs on a beach of Magdalena Island close to the mouth of the Bahia Magdalena on the Pacific coast of Baja California (Fig. 1). About 1100 hours, a compact surface swarm of live crabs was seen 1–2 m from the beach. Small groups of crabs were thrown to the beach by waves, and were unable to return to the sea.

[1] Balart-Páez, E., and Castro-Aguirre, J. L. 1992. Habitos alimenticios de la merluza Bajacaliforniana *Merluccius angustimanus*, en la costa occidental de Baja California Sur, México. Paper pres. at the IX International Symposium of Marine Biology, 1–5 June 1992, La Paz Baja California Sur, México.

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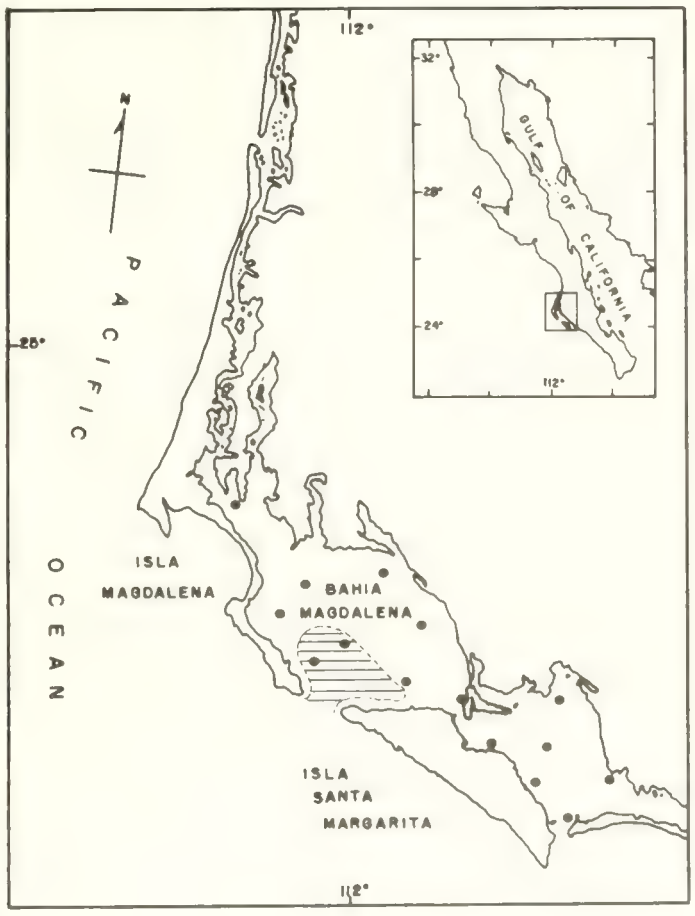

Figure 1

Study area on the west coast of Baja California Sur, México. Dots inside Bahia Magdalena indicate the location of stations sampled. The shaded area is the region where pelagic red crabs, *Pleuroncodes planipes*, were found as indicated by positive stations and visual observations (from Solís, 1991).

The general appearance of these pelagic red crabs (color and mobility) suggested that the crustaceans were healthy and that the stranding could be considered accidental (Boyd, 1962). We questioned local fishermen about crab strandings and determined that mass strandings 1) occur annually, usually in spring, from April through June, and 2) are common on Santa Margarita and Magdalena Islands but rarely seen on the peninsular coast.

Since strandings coincide with the end of the breeding season, we addressed the null hypothesis that stranded pelagic red crabs, particularly females, were in a weakened state because of energy expended in reproduction, as reported for many crustaceans (Hartnoll, 1985). It is known that pelagic red crabs are able to breed twice in a single breeding season and may produce, depending on body size, from 500 to 5000 eggs in each brood (Serrano, 1991). Based on this fact, debilitation caused by reproductive investment should be more evident in females. For that reason, the chemical composition of pelagic red crabs in Bahia Magdalena was determined for both sexes. We were aware that males were overrepresented in samples collected on the continental shelf (Boyd, 1962; Serrano, 1991); thus we also wished to determine if stranded animals were female-biased, as an explanation for the unbalanced sex ratio recorded on the continental shelf.

Materials and methods

To test whether the strandings were due to weakness caused by starvation or malnutrition, about 20 kg of live-stranded pelagic red crabs were collected as soon they were stranded. From this sample, a total of 1,150 individuals were sexed and measured for SCL to the nearest 1.0 mm. Sex was determined by the presence or absence of modified pleopods, which males use to fertilize the eggs (Boyd, 1962). Standard carapace length was measured from the antorbital notches of the rostrum to the midpoint of the posterior border of the carapace (Kato, 1974). This measurement is usually preferred over total length because it does not vary with shrinkage of the abdomen.

Stomach contents were analyzed in order to determine if 1) the animals had been feeding before stranding, and 2) the number of items and composition was similar to stomach contents of pelagic red crabs collected on the continental shelf (Pérez and Aurioles-Gamboa[2]). We examined the stomach contents from a subsample of nine individuals after fixing in formalin (4%), removing the cardiac-pyloric stomach from the animal, dissolving its contents in two drops of water and placing them on a smear slide. Pérez and Aurioles-Gamboa[2] determined that the average stomach composition in a swarm of crabs does not vary significantly after a sample of six crabs.

Food items were identified and counted under the microscope and relative abundance of major groups

[2] Pérez, F. R., and D. Aurioles-Gamboa. 1992. Cambios en la alimentación invierno-verano de la langostilla *Pleuroncodes planipes*, en la costa oeste de Baja California. Paper pres. at the IX International Symposium of Marine Biology, 1–5 June 1992. La Paz B. C. S. México.

of food items was determined. Following Pérez and Aurioles-Gamboa[2], we recorded some of the phyto and zooplankton components in four major groups: 1) phytoplankton, 2) zooplankton, 3) particulate organic matter (POM), and 4) inorganic matter (small grains of sand, clay or mud). The number of diatoms, crustacean parts, foraminifers, and other components, such as small agglomerations of POM, were counted and their numbers converted to relative frequency.

Proximate analyses was based on 200 g ♂ and 200 g ♀ of sun dried and milled pelagic red crabs (about 4 kgs of fresh crabs). The techniques used were those of the Association of Official Analytical Chemists (A.O.A.C., 1984): moisture (7.007), ash (7.009), crude fiber (7.006), crude protein (2.057), ether extract (7.060), carbohydrates (by difference from all other determinations at 100%). This methodology had been used previously to analyze pelagic red crabs sampled from the benthos of the continental shelf (Castro, 1993). Two-sample *t*-tests (Zar, 1984) were conducted to identify differences in food composition, proximate composition, and mean SCL between stranded pelagic red crabs in Bahia Magdalena and breeding pelagic red crabs collected on the continental shelf in March 1990. A chi-square test for determining a possible deviation of sex ratio was applied for the stranded pelagic red crabs (Zar, 1984).

Results

The stranded crabs formed a long brilliant red line of several kilometers on the interior coast of the northern part of Bahia Magdalena (Fig. 1). In addition, there were two lines of dried crabs separated by a few meters, higher on the beach and stranded during the previous days.

Behavior of pelagic red crabs during stranding

Two hours of observations on a surface swarm about 12 m long and 1 m wide were conducted after 1100 hours (11 May 1991) during the receding tide. The swarm was propelled to and from the beach by the waves and was unable to move offshore. When the swarm was pushed toward the beach by the wave action, some animals were thrown onto the sand and exposed as the water receded.

During sampling on the beach, the pelagic red crabs moved their legs and actively used their chelae as pincers. This behavior was typical of pelagic red crabs caught in trawls from the continental shelf. Pelagic red crabs had been caught from the shelf in all seasons, but only during mid-summer (when the bottom-surface temperature difference is as great as 17°C) did the crabs show signs of damage as they moved slowly and died rapidly on the deck (Aurioles-Gamboa, unpubl. data). In contrast, crabs were very active in the first minutes after stranding, and moved less frequently later. The crabs were brilliant red, which differentiated them from the lighter color of crabs collected on the continental shelf. Based on their vigorous activity, the pelagic red crabs stranded on Magdalena Island (Fig. 1) appeared to be in good health.

Stomach contents of stranded pelagic red crabs

The total number of items and relative frequency of the four major groups found in the stomachs is shown in Figure 2A. For comparison, the results of a typical sample taken on the continental shelf is provided in Figure 2B (Pérez, 1992). The minimum number of items counted was 457 and the maximum about 2,266. This range was greater than that found in crabs from the continental shelf (841–1,495 items). However, there was no significant difference in the mean number of items ($\bar{x}$=1,027 versus 1,100) between stomachs from the stranded crabs and those from the shelf (two sample *t*-test, $P>0.05$, df=9; $t=-0.3082$).

Food composition (particulate organic matter, zooplankton, and phytoplankton) was not different between crabs from the two regions. Inorganic matter (grains of sand, clay, etc.) was more abundant in the stomachs of the pelagic red crabs collected from the shelf ($\bar{x}$=365 versus 60; two sample *t*-test, $P<0.05$, df=9; $t=-0.0046$). This difference, however, does not account for a significant change in the feeding habits of crabs from the two samples.

Proximate composition of stranded red crabs

In stranded pelagic red crabs, the sexes were not different in protein and crude fiber (Table 1), however they differed significantly in lipids and ash contents (two sample *t*-test, $P<0.05$, df=9; $t=1.870$ and 10.012 respectively). Females had higher lipid and lower ash content than males, both by about 1.5%.

There were significant differences when the chemical composition of stranded crabs (sexes combined), were compared to crabs from the continental shelf (Table 1). Crabs from both areas were similar in their protein content, but differed in lipids and ash. The lipid content in Bahia Magdalena crabs was almost nine times higher than that in shelf crabs (*t*-test, $P<0.05$, df=16, $t=35.664$). Crabs from the continental shelf were higher in fiber and ash but lower in carbohydrate content.

It was also noted that during handling of stranded crabs an oily, orange film was left in the containers, a phenomenon not previously observed in crabs collected in more than 200 bottom trawls on the continental shelf (Aurioles-Gamboa, 1992). The substance probably contained carotenoids, which in this species have been identified as astaxanthins (Wilkie, 1972).

Size and sex of stranded pelagic red crabs

Pelagic red crabs collected in Bahia Magdalena were 12–28 mm SCL. Size distribution was similar for males and females (Fig. 3); mode and mean were 15.82 and 17.02 mm for females and 17.36 and 17.26 mm for males, respectively. Differences in mean size of males and females were statistically significant (two-sample t-test=2.057, $P<0.05$, df=1,147). In older organisms, slight sexual dimorphism is evident in males which are slightly larger and heavier with longer and wider chelae (Serrano and Aurioles-Gamboa, 1991).

Pelagic red crabs are about 14 mm SCL at the end of the first year of life (about February–March) and grow approximately 1 mm per month (Boyd, 1962). Because the crabs were about 17 mm SCL (mode), they should have been about 14–15 months old. Some individuals were about 24–28 mm SCL (Fig. 3), which according to Boyd (1962) were about 26–27 months old.

The number of females (605) in relation to the number of males (544), deviates significantly from the expected 1:1 proportion (chi-square $P<0.001$). In contrast, the sex ratio of crabs from the continental shelf is slightly male biased throughout the year (Serrano, 1991).

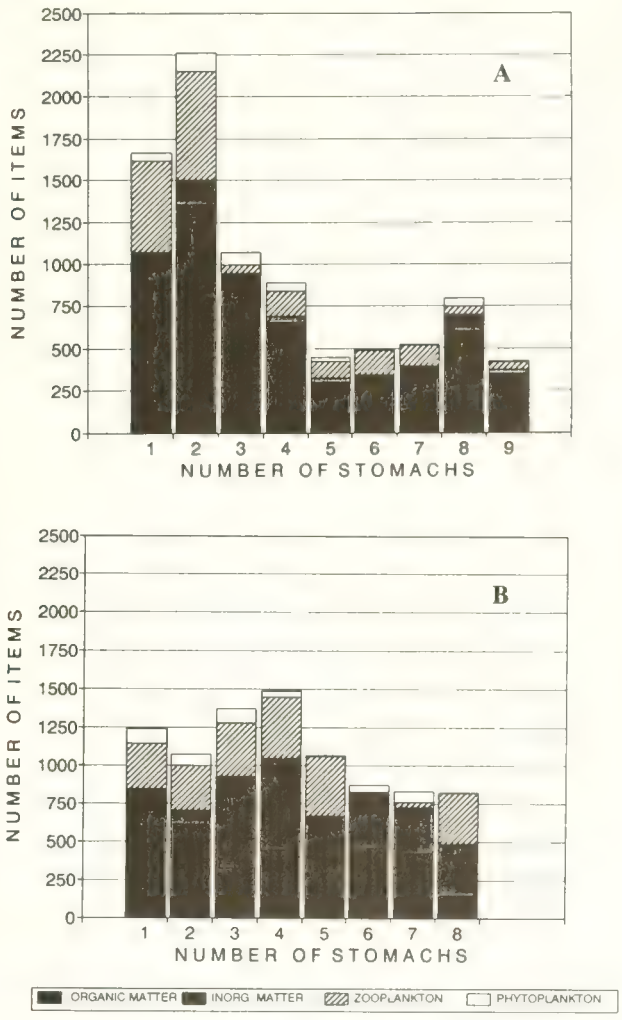

Figure 2

Total number of items and gross stomach composition from pelagic red crabs, *Pleuroncodes planipes*, collected in Bahía Magdalena (**A**), and organisms typically found on the benthos of the continental shelf off Baja California (**B**). POM = Particulate Organic Matter, IM = Inorganic Matter. Numbers below the x-axis indicate number of stomachs.

Discussion

Debilitated pelagic red crabs as explanation of strandings

We rejected the null hypothesis that stranded pelagic red crabs represent a debilitated fraction of the population because 1) the stranded crabs moved vigorously during and just after stranding, 2) the stomachs of crabs were full and the contents were similar to those collected on the continental shelf, which indicated they were feeding normally, 3) the chemical composition was generally similar to those collected on the continental shelf, and when different, did not suggest malnutrition, and 4) timing and area of strandings are better explained by physical phenomena (i.e. by accidental stranding due to funneling effect, wave action, and receding tide). Our observations support the observations made by Boyd (1962), that waves and receding tide play a major role after the animals enter the surf zone. Two available stranding reports (Boyd, 1962; Jorge Llinas[3]), indicated that beachings occurred during falling tides. According to local fishermen, the two higher lines of stranded crabs we found on the beach of Isla Magdalena on 9 May 1991, were stranded two mornings before our visit, also during receding tides.

[3] Llinas, J. Centro de Investigaciones Biologicas de Baja California Sur. Apdo. Postal 128. La Pax Baja California Sur, Mexico, personal commun. 1993.

Differences in pelagic red crab chemical composition

The lipid content of the younger stranded pelagic red crabs was different from that recorded in older specimens caught on the benthos of the continental shelf (Table 1). Differences in the proportion of chemical components between young and old individuals have been reported for many decapod species (Herring, 1973; Morris, 1973). The observed differences in lipid concentration and apparent pigmentation between young-adult and older-benthic pelagic red crabs cannot be considered abnormal or attributable to unhealthy specimens. There was no evidence to support the hypothesis of a debilitated fraction of pelagic red crabs, and strandings can be explained by mere accident.

The differences in lipid and ash content between male and female stranded crabs would be attributable to metabolic differences in which females require more lipid to invest in egg production (Hartnoll, 1985). Some females still had eggs attached on the pleopods as evidence of their reproductive condition; however, the low numbers of ovigerous females in the sample, suggested that we collected them at the end of the breeding season.

Table 1

Mean values for proximate chemical analyses of *Pleuroncodes planipes* samples from Bahia Magdalena and the Continental Shelf of Baja California.

	Bahia Magdalena				
	Males % n = 5		Females % n = 6		Significant difference 95% conf. *
Moisture	4.7	(0.28)	4.73	(0.23)	
Ash	29.79	(0.36)	28.21	(0.66)	+
Ether extract	12.79	(0.72)	15.46	(1.39)	+
Crude fiber	7.91	(0.99)	8.70	(0.65)	–
Crude protein	41.75	(0.14)	40.64	(0.07)	–
Carbohydrates	3.06		2.26		–

	Bahia Magdalena Both sexes % n = 11		Continental Shelf Both sexes % n = 12		
Moisture	4.71	(0.20)	4.12	(0.32)	
Ash	29.04	(0.24)	40.30	(0.03)	+
Ether extract	14.12	(1.98)	2.75	(0.007)	+
Crude fiber	8.30	(0.62)	12.83	(0.03)	+
Crude protein	41.19	(0.22)	38.61	(0.29)	–
Carbohydrates	2.64		1.39		–

* Two-sample *t* test for means; + significant difference, – no difference (Alpha=0.05)

Size and sex of pelagic stranded red crabs

The stranded individuals we sampled were predominantly 13 to 20 mm SCL, although some larger crabs were also found (Fig. 3). Kato (1974) also reported individuals of these two size distributions in a mass stranding in Bahia Magdalena. Photos were available of a mass stranding in May of 1979, in which pelagic red crabs larger than 25 mm SCL (second year of life, Boyd 1962) were very abundant. Therefore, the over-representation of young adults in the 1991 stranding we sampled is not the rule, as both size and age groups were found.

The sex ratio (1:1.11) of our sample was significantly female biased ($P<0.05$, $\chi^2=22.97$, df=1,147). Benthic samples of crabs in Bahía Magdalena during 1990 (Solís, 1991), also

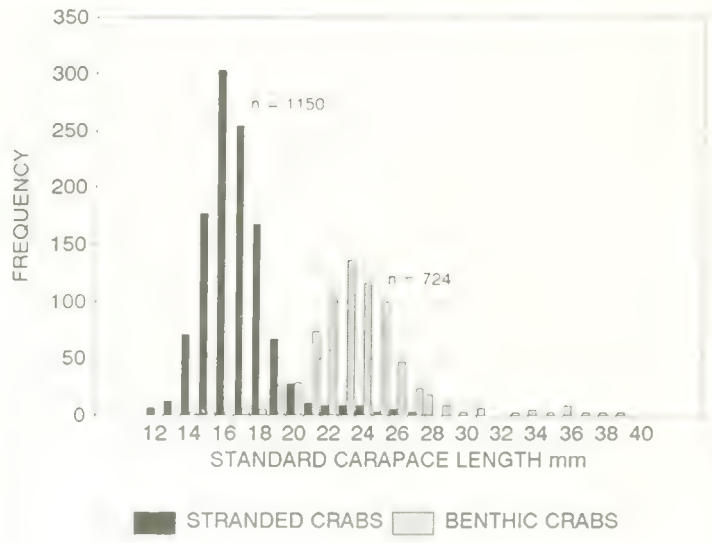

Figure 3

Size distribution of pelagic red crabs, *Pleuroncodes planipes*, stranded in Bahía Magdalena and the typical distribution of benthic crabs on the continental shelf off Baja California.

had an overrepresentation of females (1:1.23), suggesting that a higher abundance of females in stranded crabs would be a reflection of the sex ratio in the bay. Additional evidence for a female biased sex ratio in coastal waters comes from Serrano (1991), who reported higher frequency of females inshore during the breeding season. Similar findings were obtained by Escoto and Orellana (1981) for pelagic red crabs off the Nicaragua coast, and for a closely related species, *P. monodon*, from Chile (Arana and Culquichicón[4]). However, several authors have reported that the total sex ratio on the continental shelf is male biased (Boyd, 1962; Boyd and Johnson, 1963; Serrano, 1991). Boyd (1962), suggested that the sex-ratio differences on the continental shelf could be due to one or a combination of the following causes: 1) a deviation in primary sex ratio, 2) lower survival rate of females, or 3) the fact that plankton nets may not sample males and females with equal effectiveness.

The hypothesis that females die at a higher rate than males is supported by the present data, since females were more abundant where there was a natural cause of mass mortality. It has been mentioned that the breeding season of the species is synchronized to the time (winter-spring) when coastal upwelling is more intense. Pelagic red crabs may be more abundant in places where phytoplankton is more plentiful (Blackburn, 1969). Thus, it can be advantageous for pelagic red crab females to move to shore and release larvae in upwelled water. However, by doing so, females are more likely to enter Bahia Magdalena or other coastal lagoons and die in accidental strandings.

Literature cited

A. O. A. C.
1984. Official methods of analyses, 14th ed. Association of Analytical Chemists, Washington D.C.

Aurioles-Gamboa, D.
1992. Inshore-offshore movements of pelagic red crabs *Pleuroncodes planipes* (Decapoda, Anomura, Galatheidae) off the Pacific coast of Baja California Sur, México. Crustaceana 62(1):71–84.

Blackburn, M.
1969. Conditions related to upwelling which determine distribution of tropical tunas off western Baja California. U. S. Fish Wild. Serv. Fish. Bull. 68:147–176.

Boyd, C. M.
1962. The biology of a marine decapod crustacean, *Pleuroncodes planipes* Stimpson 1860. Ph.D. thesis, Univ. Calif. San Diego, 123 p.
1967. Benthic and pelagic habitats of the red crab *Pleuroncodes planipes*. Pacific Science 21:394–403.

Boyd, C. M., and M. W. Johnson.
1963. Variations in the larval stages of a decapod crustacean, *Pleuroncodes planipes*, Stimpson (Galatheidae). Biol. Bull.(Woods Hole) 124:142–152.

Castro, G. M. I.
1993. Procesos tecnologicos aplicados a la langostilla (*Pleuroncodes planipes* Stimpson) y cambios en su composición química a diferentes latitudes para su aprovechamiento en alimentación animal. Tésis de Maestría en producción animal, 82 p.

Escoto, R., and F. Orellana.
1981. Segundo crucero de evaluación del recurso langostino del Pacífico Nicaraguense. Boletín técnico del Instituto Nicaraguense de la Pesca (Diciembre 1980), 42 p.

Galván, M. F.
1988. Composición y análisis de la dieta del atún aleta amarilla *Thunnus albacares*, en el oceano Pacífico Mexicano durante el periodo 1984–1985. Tésis de Maestría en Ciencias, CICIMAR, 86 p.

Glynn, P. W.
1961. The first recorded mass strandings of pelagic red crabs, *Pleuroncodes planipes*, at Monterey Bay California since 1959, with notes on their biology. California Fish and Game 47 (1): 97–101.

Gómez, G. J.
1990. Variación de la distribución y abundancia de los estadios planctónicos de *Pleuroncodes planipes* (Crustacea: Galatheidae) en la costa occidental de Baja California Sur, México (1986). Tésis de Licenciatura en Biología Marina, Universidad Autonoma de Baja California Sur, México, 86 p.

Hartnoll, G. R.
1985. Growth, sexual maturity and reproductive output. *In* A. M. Wenner (ed.), Crustacean issues 3: factors in adult growth, p. 101–128. A. A. Balkema, Boston, and Rotterdam, Netherlands,

Herring, P. J.
1973. Depth distributions of the carotenoid pigments and lipids of some oceanic animals. 2: Decapod crustaceans. J. Mar. Biol. Assoc. U.K. 53:539–562.

Kato, S.
1974. Development of the pelagic red crab (Galatheidae, *Pleuroncodes planipes*) fishery in the eastern Pacific Ocean. Mar. Fish. Rev. 36 (10):1–9.

Longhurst, A. R., C. J. Lorenzen, and W. H. Thomas.
1967. The role of pelagic red crabs in the grazing of phytoplankton off Baja California. Ecology 48:190–200.

[4] Arana, E. P., and Z. M. Culquichicón. 1990. Estructura poblacional del langostino colorado (*Pleuroncodes monodon*) en la zona centro-sur de Chile. Estudios y Documentos. Final Rep. No. 7/89 to Universidad Católica de Valparaiso, Facultad de Recursos Naturales, Escuela de Ciencias del Mar, 56 p.

Morris, R. J.
1973. Relationships between the sex and degree of maturity of marine crustaceans and their lipid compositions. J. Mar. Biol. Assoc. U.K. 53:27–37.

Pérez, F. R.
1992. Alimentación de la langostilla *Pleuroncodes planipes* Stimpson, 1860, durante el periodo reproductivo (Marzo, 1990). Tésis de licenciatura en Biología, Universidad Nacional Autonoma de México, ENEP, Zaragoza, México, D. F., 53 p.

Serrano, P. V.
1991. Aspectos reproductivos de la langostilla *Pleuroncodes planipes* (Crustacea: Decapoda: Galatheidae). Tésis de Maestría en Ciencias Marinas, CICIMAR, 89 p, La Paz Baja California Sur, México.

Serrano, P. V., and D. Aurioles-Gamboa.
1991. Dimorfismo sexual en la langostilla, *Pleuroncodes planipes* Stimpson, 1860 (Crustacea: Decapoda: Galatheidae). Proc. of San Diego Society of Natural History 13:1–5.

Solís, F.
1991. Composición y distribución espacio-temporal de los macroinvertebrados bentónicos del complejo lagunar Magdalena-Almejas de la costa occidental de Baja California Sur. Tésis de licenciatura en Biología, Univ. Michoacana de San Nicolás de Hidalgo, México, 96 p.

Stewart, B. S, P. M. Yochem, and R. W. Schreiber.
1984. Pelagic red crabs as food for gulls: a possible benefit of El Niño. The Condor 86:341–342.

Wilkie, D. W.
1972. The carotenoid pigmentation of *Pleuroncodes planipes* Stimpson (Crustacea: Decapoda: Galatheidae). Comp. Biochem. Physiol. 42 (B):731–734.

Zar, J. H.
1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ, 716 p.

Mass marking coho salmon, *Oncorhynchus kisutch*, fry with lanthanum and cerium

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Most current salmonid tagging programs identify small proportions of a population. However, under some circumstances it is desirable to mark entire populations. Chemical marking is a technique that can rapidly mark large numbers of fish without individual handling. Marking is accomplished by exposing the fish to biologically rare elements that are subsequently incorporated and retained in certain tissues in which they are not naturally found. Marking of entire hatchery populations could be valuable from a fisheries management perspective for stock identification (hatchery versus wild salmon), assessment of contribution to fisheries, and evaluation of current tagging and sampling techniques.

Ennevor and Beames (1993) have shown that some lanthanide elements (i.e. lanthanum and cerium) are suitable for mass marking juvenile coho salmon, *Oncorhynchus kisutch*. The lanthanide elements are not absorbed from the gastro-intestinal tract (Kyker, 1961; Ellis, 1968; Luckey and Venugopal, 1977), and therefore may be introduced through the fishes' rearing water. Because these are bone-seeking elements (Durbin et al., 1956; Jowsey et al., 1958), administered lanthanides are subsequently incorporated into the bony tissues of coho salmon fry and smolts (Ennevor, 1991; Ennevor and Beames, 1993). Analysis of the vertebral column, otoliths, and scales by inductively coupled plasma-mass spectrometry (ICP-MS) revealed that administered lanthanides are present in these bony tissues 10.5 months post-treatment (Ennevor, 1991; Ennevor and Beames, 1993). ICP-MS is capable of detection and quantification of the lanthanide elements at levels as low as 0.01 $\mu g \cdot g^{-1}$ (Longerich et al., 1987; Houk and Thompson, 1988).

Trials were performed to determine whether immersion into solutions of lanthanide elements would produce recognizable marks on juvenile salmon. These studies were designed 1) to investigate differences in toxicity and uptake between the chloride and acetate forms of lanthanum and cerium, and 2) to assess optimal concentrations and exposure times for marking coho salmon fry in the extremely soft and slightly acidic water at Capilano River Hatchery, British Columbia.

Materials and methods

In the following experiments, lanthanum and cerium were introduced into the rearing water of coho salmon fry at Capilano River Hatchery. The river water at this hatchery is slightly acidic and extremely soft (pH=6.5; hardness as $CaCO_3$=3.8). Concentrated lanthanide stock solutions were metered into the tanks at a rate of 1 $mL \cdot min^{-1}$ and the rearing water was set to flow in at a rate of 1 $L \cdot min^{-1}$. The lanthanide solutions and the rearing water were mixed prior to delivery to the tanks containing the fish.

Two experiments were conducted concurrently with coho salmon fry. One hundred fry, with an average initial weight of 3.2 g, were placed in each 35-L experimental tank. Experiment 1 had 4 treatment groups and a control tank where no lanthanide was administered. The lanthanide treatments and elemental concentrations were: 50 $\mu g \cdot L^{-1}$ of $LaCl_3$, $CeCl_3$, $La(C_2H_3O_2)_3$, or $Ce(C_2H_3O_2)_3$ continuously for 24 days. Experiment 2 involved 7 treatment groups: 50 $\mu g \cdot L^{-1}$ of $La(C_2H_3O_2)_3$ or $Ce(C_2H_3O_2)_3$ continuously for a total of 24 treatment days; 100 $\mu g \cdot L^{-1}$ of $La(C_2H_3O_2)_3$ or $Ce(C_2H_3O_2)_3$ on alternate days for a total of 12 treatment days over a 24-day period; 150 $\mu g \cdot L^{-1}$ of $La(C_2H_3O_2)_3$ or $Ce(C_2H_3O_2)_3$ every third day for a total of 8 treatment days over a 24-day period; and a control tank with no lanthanum or cerium. The treatment days consisted of 24 hours of exposure. Over the treatment period, equal amounts of lanthanum or cerium were administered to each treatment group of fry at the appropriate concentration and duration.

After completion of the lanthanide exposures, the fry were provided with untreated river water for 14 days prior to sampling. Ten fry were randomly sampled from each of the tanks, body weights recorded, and the vertebral columns were removed and prepared for ICP-MS analysis to determine lanthanide accumulation. The majority of flesh was dissected away from the bony tissue and any remaining traces of flesh were digested with a 6% sodium hypochlorite solution. The clean

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backbones were oven-dried at 70°C overnight, ground to a powder, and a 0.01 g subsample from each fish was used for analysis (Ennevor, 1991; Ennevor and Beames, 1993). The prepared samples were submitted to a commercial laboratory in North Vancouver, British Columbia for ICP-MS analyses.

Experiments 1 and 2 were analyzed by analysis of variance with SYSTAT statistical software (Wilkinson, 1989) and differences between means were tested at $P \leq 0.05$ with Tukey's multiple range test. The data were pooled by treatment groups with individual fish as experimental units.

Table 1

Percent mortalities during the 24-day treatment period, mean body weights of coho salmon, *Oncorhynchus kisutch*, fry at time of sampling, mean amounts (ng) ± 1 S.E.M. of lanthanum or cerium in vertebral columns of fry marked in Experiments 1 and 2. Within experiments, mean values sharing a similar superscript letter were not significantly different ($P \leq 0.05$) according to Tukey's Test.

	Treatment group[1]				
Element	Concentration ($\mu g \cdot L^{-1}$)	Duration (d)	Mortalities (%)	Mean fry weight[2] (g)	La or Ce (ng) ± S.E.M.
Experiment 1					
La*	50	24	2	3.7	$7.0^{a} \pm 1.2$
Ce*	50	24	2	4.2	$6.1^{a} \pm 0.9$
La	50	24	0	3.5	$5.6^{a} \pm 0.8$
Ce	50	24	0	4.1	$6.2^{a} \pm 0.8$
Control	0	24	1	3.7	$0.1^{b} \pm 0.0$
Experiment 2					
La	50	24	0	3.5	$5.6^{a} \pm 0.8$
Ce	50	24	0	4.1	$6.2^{a} \pm 0.8$
La	100	12	2	2.7	$4.6^{ab} \pm 0.5$
Ce	100	12	3	3.3	$4.4^{ab} \pm 0.3$
La	150	8	12	4.1	$4.0^{b} \pm 0.5$
Ce	150	8	1	3.7	$4.0^{b} \pm 0.0$
Control	0	24	1	3.7	$0.1^{c} \pm 0.0$

[1] La* or Ce* represents the chloride forms, $LaCl_3$ or $CeCl_3$, respectively; all other treatments used the acetate forms of $La(C_2H_3O_2)_3$ or $Ce(C_2H_3O_2)_3$.
[2] Mean weights of treatment groups after 24-day treatment period and 14-day rinse period completed.

Results

Experiment 1

Lanthanum and cerium administered at 50 $\mu g \cdot L^{-1}$ daily for 24 days had no apparent deleterious effect on the fry. They appeared to be healthy and fry weights between treated and non-treated groups did not differ after the 24-day treatments and 14-day rinse were completed. Few mortalities occurred in all groups (Table 1).

Analysis of the vertebral columns from the marked fry showed each of the lanthanides to be present in approximately equal amounts. Uptake did not differ between the treatment groups. The average concentration of lanthanide in the vertebral columns was 6.1 ng of lanthanum or 6.2 ng of cerium (Table 1).

Experiment 2

Throughout the treatments, mortalities were higher in tanks that contained the 150 $\mu g \cdot L^{-1}$ treatments of lanthanum or cerium (Table 1). Fewer mortalities were observed in the 100 $\mu g \cdot L^{-1}$ treatments; none in the 50 $\mu g \cdot L^{-1}$ treatments. However, after the 24-day treatment period and 14-day rinse period were completed, fry weights did not differ between groups treated with lanthanum or cerium and nontreated groups (Table 1).

Results of the analyses of the vertebral columns from the marked fry showed a trend of significantly ($P \leq 0.05$) decreased uptake of lanthanum and cerium with decreased exposure time regardless of concentration (Table 1). Groups treated with lanthanum or cerium at 50 $\mu g \cdot L^{-1}$ daily had the greatest accumulation, whereas the groups treated with 150 $\mu g \cdot L^{-1}$ every third day had the least. In the groups treated with either element, lanthanum and cerium were accumulated in approximately equal amounts.

Discussion

Coho salmon fry were successfully marked with lanthanum or cerium that was administered through the water supply. The lanthanides were detected in the vertebral columns of marked fry, which is consistent with previous findings (Ennevor, 1991; Ennevor and Beames, 1993) and with the bone-seeking characteristics of the lanthanide elements (Durbin et al., 1956; Jowsey et al., 1958). Ennevor and Beames (1993) have shown that lanthanides that are deposited in the vertebral column, otoliths, and scales remain in these tissues for at least 10.5 months after marking. Michibata (1981) also successfully marked medaka, *Oryzias latipes*, and goldfish, *Carassius auratus*, with samarium, another lanthanide, and these fishes retained detectable amounts of the element in their scales one year after marking.

Coho salmon fry exposed to 50 $\mu g \cdot L^{-1}$ of lanthanum or cerium daily resulted in higher levels of accumulation than fry exposed intermittently to concentrations of 100 $\mu g \cdot L^{-1}$ or 150 $\mu g \cdot L^{-1}$. In tanks with higher concentrations, number of mortalities increased as deposition of the elements in the vertebral column decreased. Therefore, toxicity and accumulation may be related to element concentration during treatments rather than accumulated exposure. A high concentration of lanthanides may impair gill function and prevent further uptake of lanthanides, as well as essential ions and oxygen (Behrens Yamada and Mulligan, 1990). Consequently, marking with a low concentration of lanthanide over an extended period is highly recommended.

A potential concern is the ability to detect the lanthanide mark in the bony tissues of returning adults. Because fish continually accumulate calcium in their bony tissues after marking, the relative amount of lanthanum or cerium will decline gradually as the fish grows (Behrens Yamada et al., 1979; Behrens Yamada and Mulligan, 1982). Marks laid down during freshwater growth stages will be concentrated in the center portion of bony tissues. A possible solution to this dilution problem is to analyze only the center where the element concentration would be about the same as when marked (Behrens Yamada and Mulligan, 1982). Scales of returning adults may be more suitable for sampling and analysis as they retain higher lanthanide concentrations (Ennevor and Beames, 1993). Also, scales are easier for sampling and can be removed for lanthanide determination without sacrificing the fish.

These studies demonstrate the successful marking of experimental groups of fry with lanthanum and cerium applied through the water supply. This technique can be adapted to mark large groups of juvenile salmon at hatchery stages quickly and efficiently without affecting growth or survival. Mass marking with lanthanides can mark large groups of fish for identification without apparent deleterious effects. In addition, the mark remains in the bony tissues for extended periods of time, and samples of bony tissues (i.e. scales and opercular punches) can be taken from marked fish, without sacrificing the fish, for identification by ICP-MS analyses.

Acknowledgments

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Literature cited

Behrens Yamada, S., and T. J. Mulligan.
1990. Screening of elements for the chemical marking of hatchery salmon. Am. Fish. Soc. Symposium 7:550–561.
1982. Strontium marking of hatchery-reared coho salmon, *Oncorhynchus kisutch* Walbaum, identification of adults. J. Fish. Biol. 20:5–9.

Behrens Yamada, S., T. J. Mulligan, and S. J. Fairchild.
1979. Stontium marking of hatchery-reared coho salmon (*Oncorhynchus kisutch* Walbaum). J. Fish. Biol. 14:267–275.

Durbin, P. W., M. H. Williams, M. Gee, R. H. Newman, and J. G. Hamilton.
1956. Metabolism of the lanthanons in the rat. Proc. Soc. Exp. Biol. Med. 91:78–85.

Ellis, W. C.
1968. Dysprosium as an indigestible marker and its determination by radio-activation analysis. J. Agric. Food Chem. 16:220–224.

Ennevor, B.C.
1991. The feasibility of using lanthanide elements to mass mark hatchery-production salmon. M.Sc. thesis, Univ. British Columbia, Vancouver, B.C., 182 p.

Ennevor, B. C., and R. M. Beames.
1993. The use of lanthanide elements to mass mark juvenile salmon. Can. J. Fish. Aquat. Sci. 50:1039–1044.

Houk, R. S., and J. J. Thompson.
1988. Inductively coupled plasma mass spectrometry. Mass Spectrom. Rev. 7:425–461.

Jowsey, J., R. E. Rowland, and J. H. Marshall.
1958. The deposition of rare earths in bone. Rad. Res. 8:490–501.

Kyker, G. C.
1961. Rare earths. *In* C. L. Comar and F. Bronner (eds.), Mineral metabolism, Vol. II, Part B, p. 499–529. Academic Press, New York.

Longerich, H. P., B. J. Fryer, D. F. Strong, and C. J. Kantipuly.
1987. Effects of operating conditions on the determination of the rare earth elements by inductively coupled plasma mass spectrometry (ICP-MS). Spectrochim. Acta 42B:75–92.

Luckey, T. D., and B. Venugopal.
1977. Lanthanides, the rare–earth metals. *In* T. D. Luckey and B. Venugopal (eds.), Metal toxicity in mammals, Vol. II. Plenum Press, New York.

Michibata, H.
1981. Labeling fish with an activable element through their diet. Can. J. Fish. Aquat. Sci. 38:1281–1282.

Wilkinson, L.
1989. SYSTAT: the system for statistics. Systat, Inc., Evanston, IL, 822 p.

Distribution and relative abundance of the blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean

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The blue shark, *Prionace glauca*, is one of the most abundant oceanic-epipelagic sharks and is probably the widest ranging chondrichthyian (Compagno, 1984). It is frequently caught by tuna longline fisheries in temperate, subtropical, and tropical waters of the world oceans (Pratt, 1979).

Hazin et al. (1990) investigated the distribution and abundance of pelagic sharks caught from 1983 until 1988 by Brazilian longliners in the southwestern equatorial Atlantic. Blue shark and sharks of the genus *Carcharhinus* were the dominant species, together representing nearly 95% of the shark catches (Hazin et al., 1990). They reported that blue shark abundance had a marked seasonal fluctuation with the highest catches taking place during the third and fourth quarters of the year and the lowest in the first quarter.

The objective of the present study is to further investigate the distribution and relative abundance of the blue shark, *Prionace glauca*, in the south-western equatorial Atlantic Ocean, including the following aspects: a) seasonal fluctuation of catch per unit of effort (CPUE) as related to sea surface temperature; b) sex, and size and age composition of blue shark catches; c) vertical distribution as related to the vertical temperature profile.

Material and methods

This study was based on shark catches during 50 fishing cruises by a commercial tuna longliner, FV *Argus*, from August to December 1987 and from February 1990 to December 1991. On 325 longline operations during these cruises, a total of 992 blue sharks were caught. The commercial longline consisted of 120 baskets, each with 7 branch lines. The bait was frozen Brazilian sardine, *Sardinella brasiliensis*. Average local time of set, retrieval, and mean soaking time of the longline is shown in Table 1. Further details of longline fishing gear and methods were described in Hazin (1986).

The fishing ground was located between lat. 2°S and 7°S and long. 32°W and 38°W. Fishing areas were divided into segments of 1° latitude × 1° longitude. The central positions of the 325 longline sets (Fig. 1) were calculated as the average latitude and longitude of the beginning and end of set and retrieval. Distribution of fishing effort by month is presented in Table 2. Blue shark relative abundance was expressed as average catch, in number of fish, per 100 hooks (CPUE). The mean CPUE was calculated as the total catch, in number of fish, divided by the total fishing effort, in 100 hooks. The distribution of blue shark mean CPUE by segments of 1° latitude × 1° longitude was observed and its relation to ocean depth analyzed. Ocean depths for each longline set were calculated as the weighted mean of the three closest values read from the nautical chart number 50, issued by the Brazilian Navy.

The monthly fluctuation of CPUE and sex ratio was analyzed and compared to sea surface temperature. An analysis of variance

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(ANOVA) was performed to determine whether blue shark CPUEs were significantly different among months. The mean CPUE for each month was calculated and all monthly mean CPUEs were then compared by ANOVA, through one-way classification of data. The months were the only independent variable (Table 3). No CPUE data were available from October 1990 and from January and April 1991. Data on the sex of the specimens were not available from January to October 1991.

All lengths are reported as fork length (FL), which was measured from the tip of the snout to the fork of the tail. Blue sharks were always measured at the time of landing. Length data were available only for 1990 and 1991. To better understand seasonal variation in CPUE, CPUE data for the various age classes of male specimens from February through December 1990 were evaluated. Females were not included because they were present only from February to July. To calculate the age-CPUE distribution, male blue shark lengths were converted to age by Stevens' (1975) growth equation, as follows:

$$Lt = 423\,(1-e^{-0.11(t+1.035)})$$

Table 1

Average set, retrieval and soaking time (in decimals) with standard deviations, for longline operations of FV *Argus* from February to December 1990.

		Local time	Standard deviation
Set	Beginning	1.61	0.58
	End	4.00	0.53
Retrieval	Beginning	10.31	1.47
	End	17.52	1.68
Soaking time (hours)		11.11	1.54

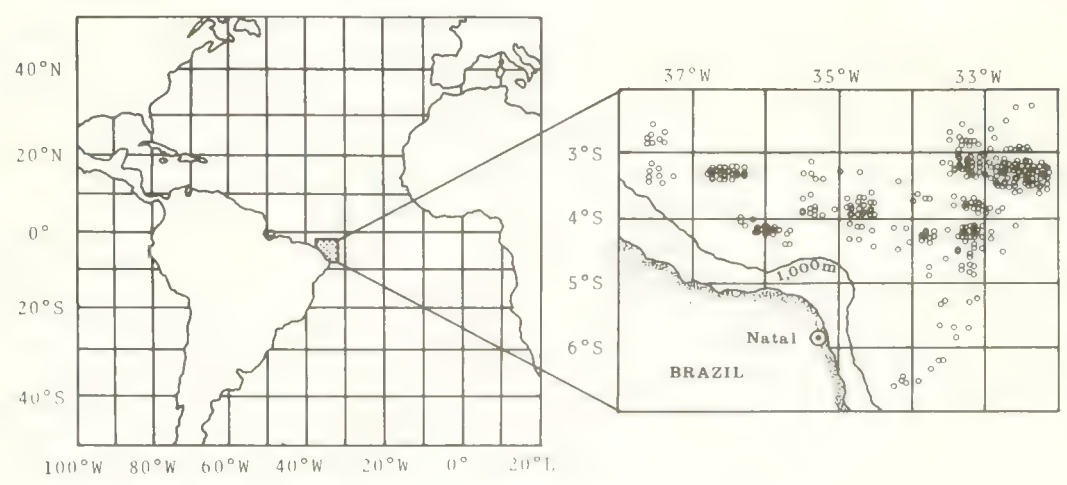

Figure 1

Location of the fishing ground (hatched area) and central positions of the longline sets made by the FV *Argus* from August to December 1987 and from February 1990 to December 1991, in the southwestern equatorial Atlantic Ocean.

Table 2

Distribution of fishing effort of FV *Argus* by months, from August to December 1987 and from February 1990 to December 1991, in the southwestern equatorial Atlantic Ocean.

	Jan.	Feb.	Mar.	Apr.	May	Jun	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
No. of sets	16	12	23	15	27	24	23	32	36	44	39	34	325
%	5	4	7	5	8	7	7	10	11	13	12	11	100

where Lt = total length, and t = age in years. Fork length data were converted to total length by the regression of Hazin et al. (1991):

$$FL = 11.27 + 0.78\ TL$$

where FL = fork length, and TL = total length.

Depths of longline hooks were estimated using the equations of Yoshihara (1952, 1954, a and b). Vertical distribution of males and females was studied through the relative distribution of mean catches on longline hooks, during February to June and July to December 1990. Differences in mean catch of males and females on longline hooks were evaluated by chi-square analysis (df=6). Sea water temperature from 0 to 300 m was surveyed in 35 DBT (digital bathythermograph) profiles: 6 in May 1990, 3 in May 1991, 5 in June 1991, 13 in November 1990, 2 in November 1991, and 6 in December 1990. From January to December 1990, sea surface temperature was measured by a mercury thermometer.

Results

From August to December 1987 and from February 1990 to December 1991, the blue shark mean CPUE by quadrates increased eastward, being particularly high east of long. 35°W (Fig. 2). Of the 325 sets, 260 (nearly 80%) were over bottom depths greater than 1,000 m. In these areas, the mean CPUE of blue shark was 0.50. The remaining 65 sets were in areas with depths shallower than 1,000 m, close to oceanic banks (Aracati, Sirius, and Guara banks), and west of 35°W. In these areas, the mean CPUE of blue shark was only 0.05.

The fluctuation of the monthly mean CPUE of blue shark in the area east of 35°W, over ocean depth of 1,000 m, for 1987, 1990 and 1991, were similar (Fig. 3). In 1990 and 1991 the CPUE was low until May, increased during June and July, decreased again in August, increased during September and October, and decreased once more in November and December. In 1987 the CPUE was low in August, increased in October and decreased during November and December. Differences in mean CPUE among months were significant (ANOVA; $P<0.0001$; Table 3).

The fluctuation of the monthly mean CPUE of male and female blue sharks was distinct (Fig. 4). CPUE for females was highest during March. From July to December, CPUE for females was low in this fishing ground. CPUE for males, however, was lowest during March, after which abundance increased and peaked during September and October. The sea surface temperature in 1990 was highest in May and lowest in September. During this year, in general, the CPUE of males tended to decrease with an increase in the sea surface temperature, whereas the CPUE of females tended to increase.

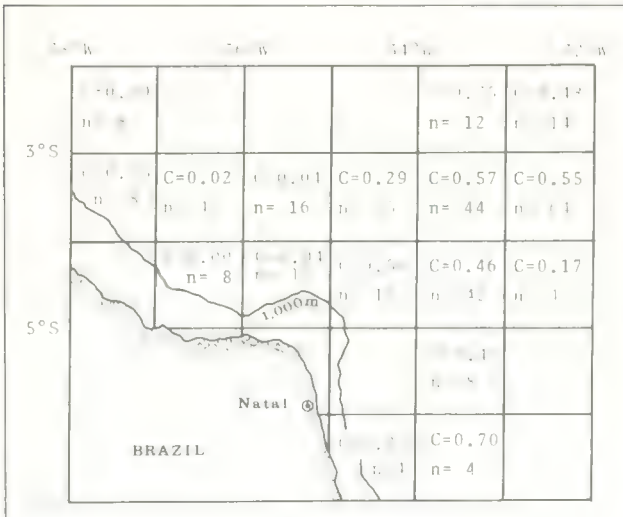

Figure 2

Mean catch per 100 hooks (CPUE) of blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean, from August to December 1987 and from February 1990 to December 1991. C= CPUE; n= number of longline sets.

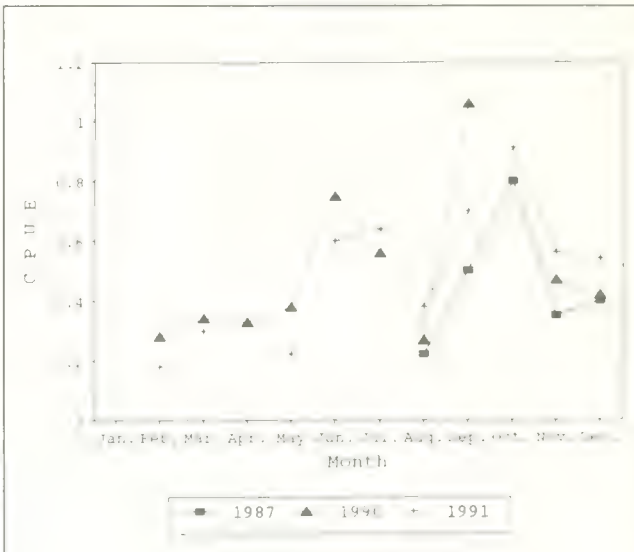

Figure 3

Monthly mean catch per 100 hooks (CPUE) of blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean, in the area east of long. 35°W and with ocean depth over 1,000 m, from August to December 1987 and from February 1990 to December 1991.

Of 810 specimens, 652 (about 80%) were male and 158 were female (about 20%). Overall, the sex ratio (male/female) for the entire period was 4.12:1. The sex ratios for each month are given in Table 4.

Females ranged in size from 162 to 226 cm and males from 156 to 250 cm (Fig. 5). Seasonal fluctuation in male CPUE during 1990 was different among age groups (Fig. 6). From February to May, ages ranged from 4.5 to 8.5 years, with most (83%) individuals between 6 and 8.5 years old (83%). The CPUE rise in June–July was due to an increase in the same age classes as from February–May. Some older specimens from 9 to 10.5 years also appeared. The CPUE of fish younger than 7 years decreased markedly in August. During September–October the CPUE of ages 7.5 to 10 increased sharply. In November–December the CPUE of age classes from 7.5 to 8.5, and also 9.5, were reduced, whereas the CPUE of other age classes did not change much. From February to July, younger fish (4.5 to 7.5 years) were more abundant than from August to December, their CPUE being particularly high in June–July. From August to December, fish older than 7.5 years had a higher CPUE than in the previous months, with a peak in September–October.

The calculated depth of longline hooks during 137 longline fishing operations of 1990 ranged from 87 to 206 m (Table 5). The figures given in this table approximate the actual depths of longline hooks. The most striking feature of the DBT profiles is the pres-

Table 3

Analysis of variance (ANOVA) and expected mean squares for comparison of monthly mean CPUEs of blue sharks, *Prionace glauca*, caught by the FV *Argus*, during 325 longline sets, from August to December 1987 and from February 1990 to December 1991, in the southwestern equatorial Atlantic Ocean.

Source of variation	Degrees of freedom	Sum of squares	Mean squares	*F*	*P*
Month	24	11.41	0.48	4.65	<0.0001
Error	300	30.68	0.10	—	—
Total	324	42.09	—	—	—

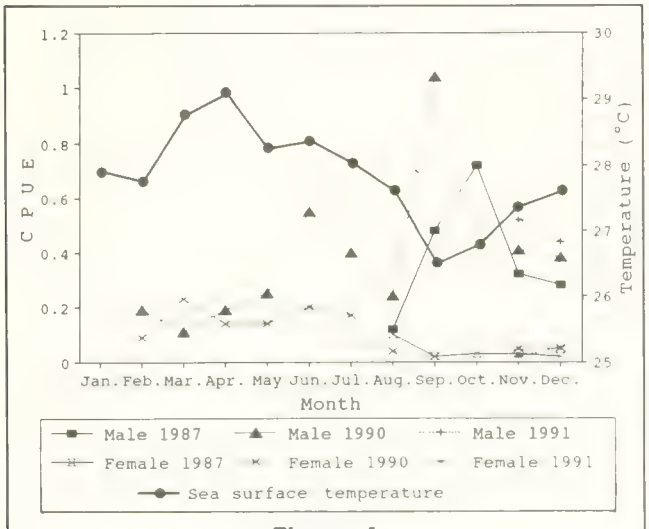

Figure 4

Monthly mean sea surface temperature in 1990 and monthly mean catch per 100 hooks (CPUE) of male and female blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean, from August to December 1987 and from February 1990 to December 1991.

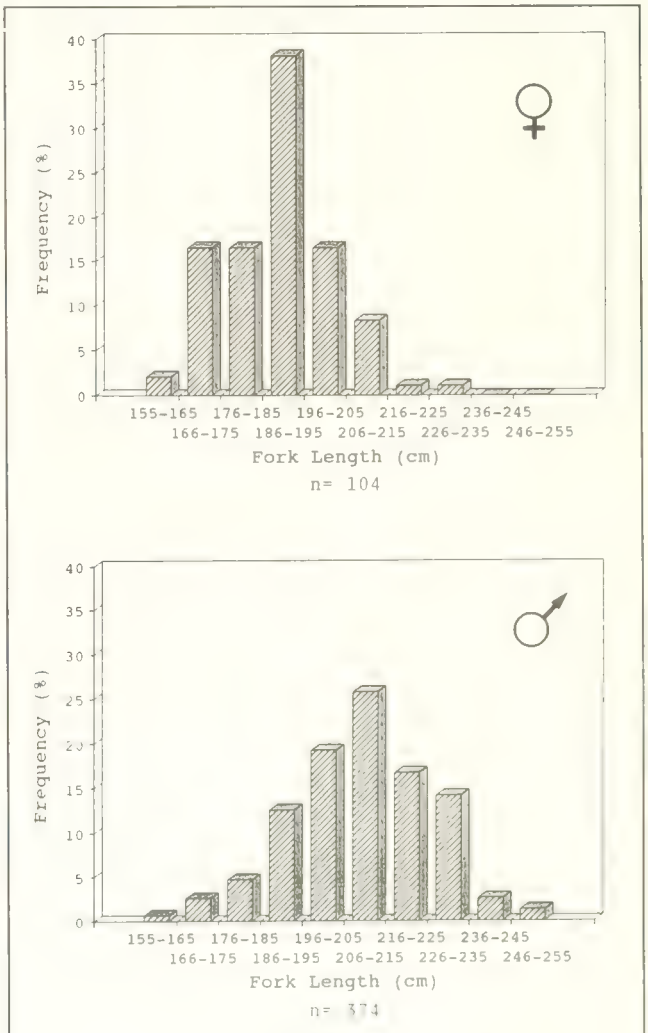

Figure 5

Length-frequency distribution of male and female blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean, from February to December 1990 and November to December 1991. Males: n = 374; min. = 156 cm; max. = 250 cm. Females: n = 104; min. = 162 cm; max. = 226 cm.

ence of a steep thermocline during the entire year. The range and mean of sea water temperature at the calculated depths of longline hooks, and the mean depth and temperature at the top and bottom of the thermocline in May–June and November–December are shown in Table 6. All longline hooks were located in or below the thermocline (Fig. 7). During Nov.–Dec. the thermocline was about 30 m deeper than during May–June.

Male blue shark catches from February to June were concentrated among central, deeper hooks, whereas in the second half of the year they were more uniformly distributed (Fig. 8). Male catch was significantly different among hooks from February to June (chi-square; $P<0.005$), but not from July to December ($0.10 < P<0.25$). The difference of male catches, on hooks 3, 4, and 5 between February-June and July-December was significant ($0.05 < P<0.10$). The relative distribution of female blue shark catches along longline hooks from February to July (Fig. 8) was different from that of males; the highest catches took place on hooks 2 and 5. The difference between male and female catches among hooks during February to July was significant ($0.01 < P<0.05$). The distribution of male and female catch among hooks suggests that males were distributed in shallower waters between July and December than between February and June and that females from February to July had a shallower distribution than males.

From February to July, CPUE for females was highest in hooks 2 and 5 (130 to 165 m), and CPUE for males in hooks 3 and 4 (165 to 180 m) (Table 5). The corresponding range of sea water temperature was 13.8° to 20.4°C for females and 12.9° to 17.1°C for males (Table 6). Male catch among hooks from July to December, was much more uniform, suggesting a depth range for males from 90 to 180 m (Table 5), or from about 15° to 28°C (Table 6), up to the top of the thermocline (Fig. 7).

Table 4

Blue shark, *Prionace glauca*, monthly sex ratio (number of males per female), in the southwestern equatorial Atlantic Ocean.

Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
2.08	0.48	1.29	1.79	2.71	2.35	6.00	54.00	25.00	16.00	8.50

Table 5

Mean and range of calculated depths (m) of longline hooks, during 137 longline operations, in the southwestern equatorial Atlantic Ocean, from February to December 1990.

Hook no.	Mean depth	Minimum	Maximum
1 and 7	92.66	87	96
2 and 6	131.56	120	140
3 and 5	164.19	145	181
4	179.20	154	206

Discussion

The results on horizontal distribution agree with those of Hazin et al. (1990), corroborating the oceanic character of blue shark (Fig. 2). Abundance was also clearly related to bottom depth. The mean CPUE of blue shark in areas of bottom depths greater than 1,000 m was 10 times higher than in shallower areas. The lower abundance of blue sharks west of 35°W

Table 6

Range and mean of sea water temperature (°C) at calculated depths (m) of longline hooks 1 to 7 and mean depth and temperature at the top and bottom of the thermocline, as inferred from 35 DBT (digital bathythermograph) surveys carried out in May–June and November–December 1990 and 1991, in the southwestern equatorial Atlantic Ocean.

	Hook number				Thermocline			
					Top		Bottom	
Month	1 and 7	2 and 6	3 and 5	4	Depth.	Temp.	Depth.	Temp.
May–June								
Temp. mean	22.6	16.3	14.8	13.2	55	28	120	13.5
Temp. range	18.5–25.7	13.8–20.4	13.1–17.1	12.9–13.3				
Nov.–Dec.								
Mean	27.6	17.0	15.4	14.9	85	27	130	15.5
Range	26.8–29.1	14.3–24.0	14.0–20.1	13.9–18.6				

(Fig. 2), therefore, is probably a consequence of ocean depth, because almost all sets performed in this fishing ground took place in shallow depths and in the vicinity of oceanic banks.

The monthly mean CPUEs of males and females (Fig. 4) show that the higher relative abundance of blue shark during the third and fourth quarters of the year (Hazin et al., 1990) is mostly comprised by males. These results indicate also that males and females are segregated and that their migratory movements are different. The different seasonal fluctuation of CPUE for different male age groups indicate that male specimens were also segregated by size. The use of Stevens' (1975) growth equation to calculate these ages from fork length may have limitations because it is based on data from the North Atlantic Ocean. Nevertheless, Amorim (1992) studied the growth of blue shark in the south-western Atlantic and found a value of k= 0.1126, which approximates Stevens' value of 0.11.

Differences in vertical distribution displayed by male and female blue sharks (Fig. 8) indicate that vertical sexual segregation likely occurred in the first half of the year. They also suggest that the depth range of male blue sharks may change seasonally.

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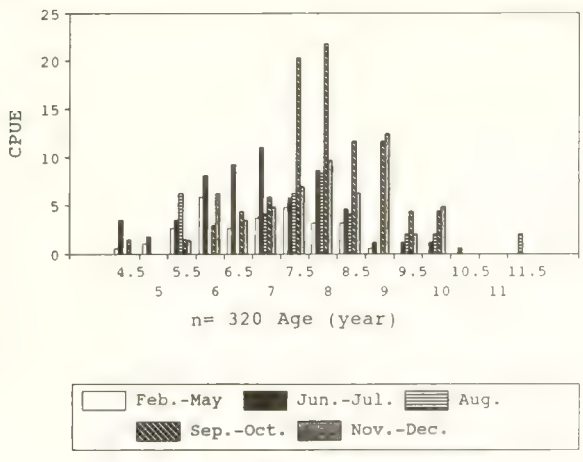

Figure 6

Mean catch per 10,000 hooks of male blue shark, *Prionace glauca*, by age classes, from February through December 1990, in the southwestern equatorial Atlantic Ocean. n = 320.

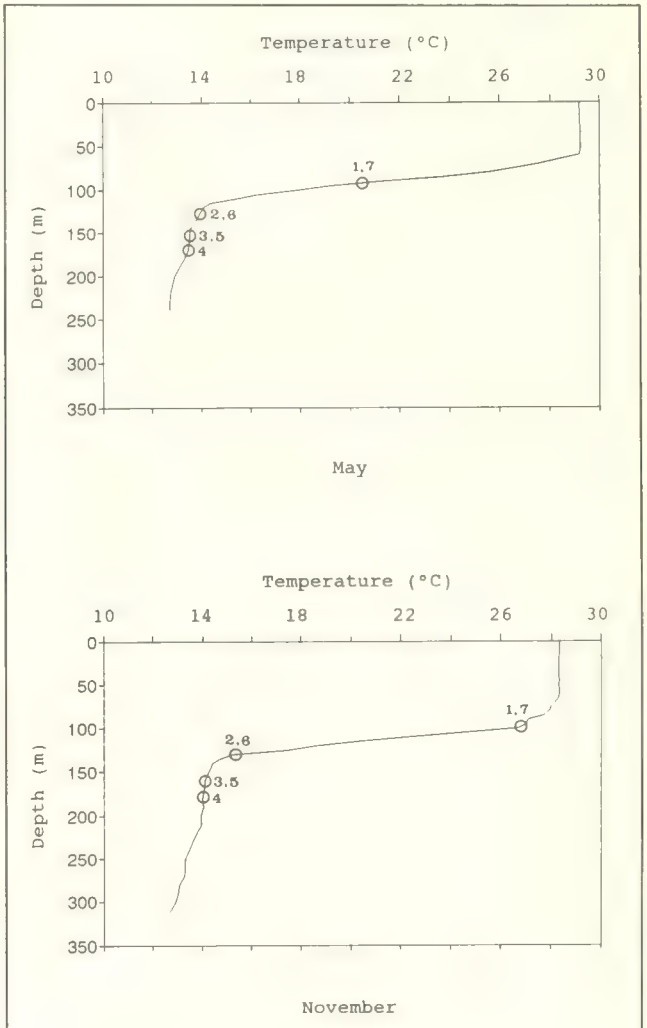

Figure 7

Typical temperature profiles for May and November, in the southwestern equatorial Atlantic Ocean, and the calculated mean depths of the hooks 1 to 7 of the longline of the FV *Argus*.

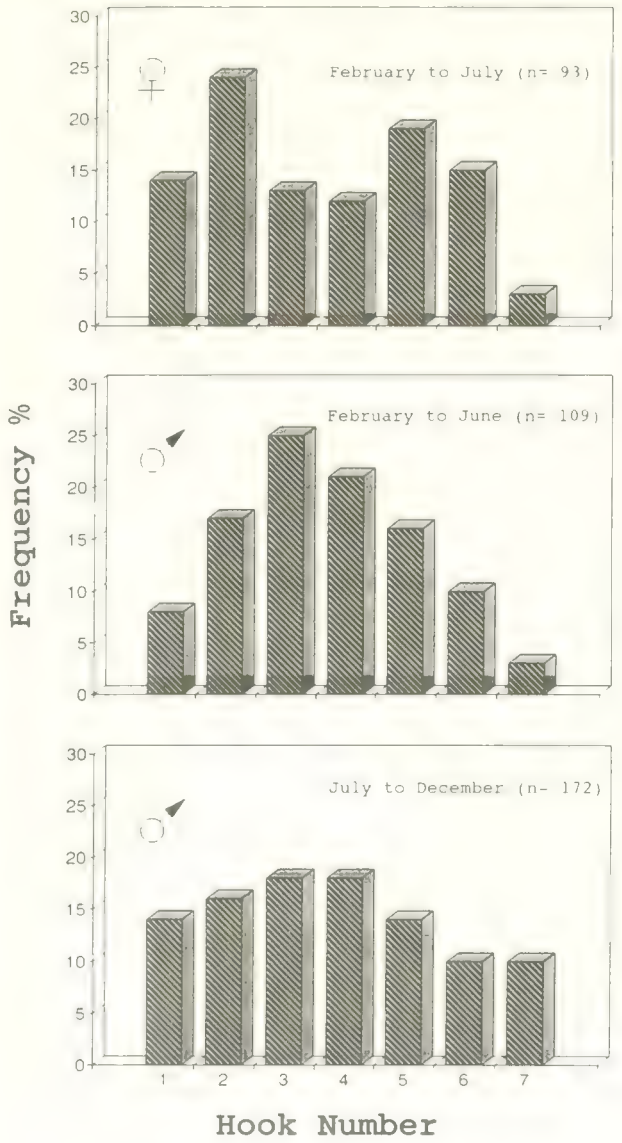

Figure 8

Male and female blue shark, *Prionace glauca*, catch-frequency distribution along the hooks of the longline, in the southwestern equatorial Atlantic Ocean, during February to June and July to December, 1990.

Literature cited

Amorim, A. F.

1992. Estudo da biologia, pesca e reprodução do cação azul, *Prionace glauca* L. 1758, capturado no sudeste e sul do Brasil. Ph.D. thesis, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil, 176 p.

Compagno, L. J. V.

1984. FAO species catalogue. Vol. 4, Parts 1 and 2: Sharks of the world: an annotated and illustrated catalogue of shark species known to date. FAO Fish. Synop. 125, 655 p.

Hazin, F. H. V.

1986. Pesca de atuns e afins com embarcação de pequeno porte no nordeste brasileiro. Graduation thesis, Universidade Federal Rural de Pernambuco, Recife, Brazil, 107 p.

Hazin, F. H. V., A. A. Couto, K. Kihara, K. Otsuka, and M. Ishino.

1990. Distribution and abundance of pelagic sharks in the south-western equatorial Atlantic. J. Tokyo Univ. Fish. 77(1):51–64.

Pratt, H. L., Jr.

1979. Reproduction of the blue shark, *Prionace glauca*. Fish. Bull. 77:445–470.

Stevens, J. D.

1975. Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). J. Mar. Biol. Assoc. U.K. 55:657–665.

Yoshihara, T.

1952. Distribution of catches of tuna longline. III: Swimming depth. [In Japanese.] Nippon Suisan Gakkaishi, 18(8):187–190.

1954a. Distribution of catches of tuna longline. IV: On the relation between K and psi with a table and a diagram. [In Japanese.] J. Tokyo Univ. Fish. 19(10):1012–1014.

1954b. On the distribution of catches by tuna longline. J. Tokyo Univ. Fish. 41(1):1–26.

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Errata

Thompson, Grant G.
Variations on a simple dynamic pool model
Fish. Bull. 91(4):718–731

Equation 1 should read as follows:

$$w(a) = w_r\left(\frac{a-a_0}{a_r-a_0}\right)$$

Equation 26 should read as follows:

$$B_f(F') = \left(\frac{b(F',a_f)}{M}\right)\left(\frac{1+K_f''+F'}{(1+F')^2}\right)$$

Appendix Equation A5 should read as follows:

$$BPR(F') = \int_{a_r}^{\infty} w_r\left(\frac{a-a_0}{a_r-a_0}\right)^n e^{-M(1+F')(a-a_r)}da$$

$$= \left(\frac{w_r}{M}\right)\sum_{k=0}^{n}\frac{(n)_k K''^k}{(1+F')^{k+1}}.$$

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Volume and page numbers for the following citation should be corrected to read as follows:

Thompson, G. G.
1992. Management advice from a simple dynamic pool model. Fish. Bull. 90:552–560.

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Environmentally induced recruitment variation in petrale sole, *Eopsetta jordani*

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Abstract.—Potential effects of parental stock size and environmental factors on year-class strength (YCS) of petrale sole, *Eopsetta jordani*, were investigated in two areas off Oregon and Washington (Pacific States Marine Fisheries Commission areas 2B: 42°50'N–44°18'N, and 3A: 45°46'N–47°20'N). Parental egg production indices and YCS were not consistently correlated over the period 1970 to 1977. Variation in YCS between 1958 and 1977 was associated with oceanographic conditions from winter to early spring, the period in which pelagic larval stages are most abundant. A regression model based on indices of offshore Ekman transport from January to March and alongshore transport from December to February accounted for nearly 55% of the YCS variation in Area 2B. In Area 3A, the previous two indices plus sea surface temperature from December to February explained about 65% of the YCS variation. Inshore advection of eggs and larvae could favor settlement of juveniles into nearshore areas and increase the subsequent recruitment strength of petrale sole.

Manuscript accepted 8 December 1993.
Fishery Bulletin 92:481–493 (1994).

Recruitment fluctuations in fish populations are ascribed to many physicochemical factors and biological processes, including parental stock size and fishing (Ricker, 1975; Shepherd et al., 1984). However, the importance of various factors to the recruitment of most species of fish is virtually unknown. Although year-class strength (YCS) of many fishes is thought to be determined at the egg and larval stages (Sharp[1]; Rothschild and Rooth, 1982), it may also be significantly affected during the postlarval stages (Smith, 1981; Sissenwine, 1984).

Increasing evidence suggests that oceanographic conditions affect the recruitment of many fishes in the Northeast Pacific Ocean (e.g. Parrish et al., 1981; Bailey and Incze, 1985; Hollowed et al., 1987; Botsford et al., 1989). A recent hypothesis suggests that recruitment of groundfish off the west coast of the United States is related to the timing of the spring transition, a period of major changes in oceanographic conditions.[2] On the Oregon–Washington shelf oceanographic conditions exhibit strong seasonal patterns (e.g. Huyer et al., 1975; Halpern, 1976; Huyer, 1977; Landry et al., 1989). In winter, alongshore currents are northward at all depths, and cross-shore surface currents flow inshore resulting in downwelling. In spring, flow is southward at all depths but stronger near the surface. The spring transition usually occurs within a one week period during March or April (Strub et al., 1987; Strub and James, 1988). In summer, a surface coastal current flows southwestward and the attendant offshore transport causes upwelling; however, deep flow is northward. In fall, alongshore currents are northward at all depths.

Petrale sole, *Eopsetta jordani*, Pleuronectidae, is a commercially important flatfish of the northeast Pacific Ocean (Ketchen and Forrester, 1966). It is continuously distributed from the Bering Sea (58°N–152°W) to Baja California (32°26'N–117°16'W) (Roedel, 1953; Hitz and

[1] Sharp, G. D. 1980. Report of the workshop on effects of environmental variation on survival of larval pelagic fishes. *In* Sharp, G. D. (rapporteur), Report and supporting documentation of the workshop on the effects of environmental variation on the survival of larval pelagic fishes, p. 15–59. Int. Ocean. Comm. Workshop Rep. 28.

[2] Lynn, R. J. Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038. Personal commun., 1991.

Rathjen, 1965). Recruitment fluctuations of petrale sole appear to be strongly related to environmental factors (Ketchen and Forrester, 1966). Ketchen (1956) demonstrated a positive correlation between winter sea surface temperature and recruitment of petrale sole off British Columbia from the middle 1940's to the middle 1950's. In the same area, Ketchen and Forrester (1966) postulated that warmer sea surface temperatures and onshore transport of pelagic early life stages could favor recruitment of this species.

Two central spawning areas of petrale sole, Heceta Bank and Willapa Deep, are located off Oregon and Washington (Fig. 1). Petrale sole spawn from late fall to early spring at depths of about 300–450 m (Cleaver, 1949; Harry, 1959; DiDonato and Pasquale, 1970; Pedersen, 1975). The incubation period of newly fertilized eggs ranges from about 6 to 13 days (Alderdice and Forrester, 1971). The eggs and yolk-sac larvae are stenohaline and stenothermal (Alderdice and Forrester, 1971). Development of pelagic eggs and larvae occurs mainly from winter to spring, followed by the presettlement and postsettlement juvenile stages from summer to fall respectively (Fig. 2). Although petrale sole larvae have been found from 2 to 120 km offshore, Pearcy et al. (1977) collected nearly 50% of them 83–120 km offshore. However, postsettlement juveniles have only been found at 18–90 m depth in the inner continental shelf (Ketchen and Forrester, 1966; Gregory and Jow, 1976; Pearcy et al., 1977).

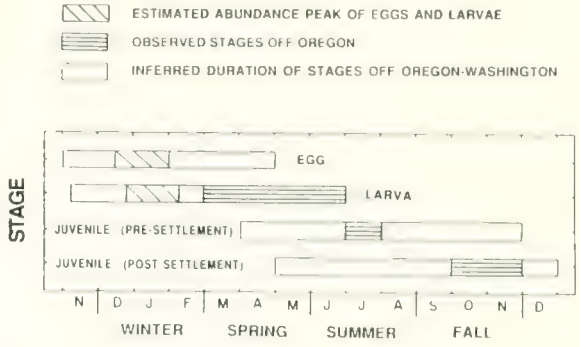

Figure 2

Estimated duration of life stages of petrale sole, *Eopsetta jordani*, off Oregon and Washington from the beginning of the spawning period to the time in which most age-0 juveniles are found settled in the inner continental shelf. The inferred temporal occurrence of life stages was based on the reported duration of spawning, incubation period and presence of presettlement and postsettlement juveniles in the Northeast Pacific Ocean (based on Cleaver, 1949; Harry, 1959; Best, 1963; Porter, 1964; Ketchen and Forrester, 1966; Alderdice and Forrester, 1971; Gregory and Jow, 1976; and Pearcy et al., 1977).

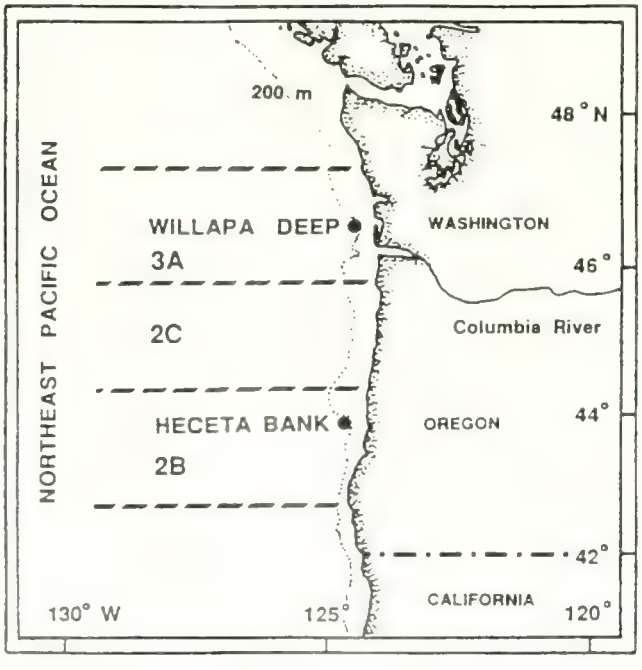

Figure 1

Location of Willapa Deep and Heceta Bank spawning grounds of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 3A and 2B. Spawning areas are located nearly 50 km offshore (modified from Pedersen, 1975).

The recruitment patterns of petrale sole off Oregon and Washington demonstrated consecutive series of cohorts alternating between below average (weak) YCS and above average (strong) YCS over the base period 1958–77 (Castillo, 1992). Possible causes for such recruitment variations have not yet been studied. Our objectives were to determine 1) if spawning biomass of petrale sole is correlated with YCS, 2) if YCS fluctuations are associated with selected environmental factors, and 3) the percentage of YCS variation explained by environmental factors.

Data and methods

We selected two locations off Oregon and Washington to investigate the effect of environmental factors on YCS of petrale sole: Pacific States Marine Fisheries Commission[3] areas 2B (42° 50'N–44°18'N) and 3A (45°46'N–47°20'N) (Fig. 1). Indi-

[3] Named Pacific Marine Fisheries Commission (PMFC) areas until 1990.

ces of YCS for petrale sole were obtained from cohort analyses of numbers of females recruited to six years of age in areas 2B and 3A (Table 1). These YCS indices represent the recruitment strength of year classes hatched from 1958 to 1977. Males were excluded from these YCS indices because of problems of increasing age underestimation in fish over 8 years.[4] However, because recruitment variation was similar in males and females of younger age groups, the YCS indices should be representative of both sexes.

Potential egg production was used as a proxy for spawning biomass (e.g. Hayman and Tyler, 1980). Egg production was estimated from fecundity and maturity information (Porter, 1964) and from cohort analyses of the parental stock for years 1970 to 1977 (Castillo, 1992). Annual potential egg production was estimated as the sum of the age-specific products of the numbers of females, their fecundity, and their percent maturity. The number of females was estimated from the observed annual sex ratio in the commercial landings. Females composed on average 58% of petrale sole landed. Egg production was averaged for fish over age 13 years because of the scarcity of older females.

Eight environmental indices available within, or near, areas 2B and 3A were used to investigate possible correlations with petrale sole YCS (Table 2). Ocean transport calculations provided by The Pacific Fisheries Environmental Group (PFEG) were based on Bakun (1973; after Fofonoff[5]). Sverdrup transport was calculated by PFEG by using a finite difference form of equation six in Nelson (1977)[6]. A proxy for salinity was based on observations of water density at constant temperature available at the Columbia River estuary (Table 2, Fig. 1). The timing of the spring transition was obtained from Strub and James

[4] Recent use of the break-and-burn technique for aging otoliths showed that males grow more slowly and lay down less year-marks (annuli) on the surface of the otolith than females (William H. Barss, Oregon Department of Fish and Wildlife, Newport, OR 97365, unpubl. data).

[5] Fofonoff, N. P. 1960. Transport computations for the North Pacific Ocean—1958. Fish. Res. Board Can. Manuscr. Rep. Oceanogr. and Limnol. No. 80.

[6] $M_y = \hat{k}(\nabla \times \vec{\tau})/\beta$ where: M_y is the meridional component of the vertically integrated mass transport, $\hat{k}(\nabla \times \vec{\tau})$ is the vertical component of the wind stress curl, and β is the meridional derivative of the Coriolis parameter.

Table 1

Cohort analyses of numbers of female petrale sole, *Eopsetta jordani*, reaching 6 years of age in Pacific States Marine Fisheries Commission areas 2B and 3A (Castillo, 1992; after Jones, 1981). Both year-class strength indices were significantly correlated with Summed-CPUE indices ($P \leq 0.05$, Castillo, 1992; after Hayman et al., 1980).

Cohort (year)	Year-class strength (thousands of fish)	
	Area 2B	Area 3A
1958	208	543
1959	278	544
1960	309	624
1961	385	692
1962	231	333
1963	296	421
1964	240	365
1965	280	547
1966	487	954
1967	352	703
1968	419	737
1969	349	558
1970	426	651
1971	421	570
1972	373	463
1973	356	415
1974	259	326
1975	193	332
1976	157	286
1977	223	424

Table 2

Environmental indices used in correlations with year-class strength of petrale sole, *Eopsetta jordani*. Recruitment areas include Pacific States Marine Fisheries Commission areas 2B and 3A. (Source of data is indicated for each environmental factor.)

Environmental index	Recruitment area
Sea surface atmospheric pressure[1, 3]	2B, 3A
Alongshore coastal transport indices	
Mean sea level[2]	
Neah Bay (48°22'N–124°38' W)	3A
Crescent City (41°45'N–124°12' W)	2B
Northward Ekman transport[1, 3]	2B, 3A
Northward Sverdrup transport[1, 3]	2B, 3A
Offshore Ekman transport[1, 3]	2B, 3A
Cube of wind speed[1, 3]	2B, 3A
Water properties	
Sea surface temperature[3]	
(43°N–44.9°N), (124°W–124.9°W)	2B
(46°N–47.9°N), (124°W–124.9°W)	3A
Salinity index Columbia River[2]	
Estuary (46°13'N–123°45'W)	2B 3A

[1] Computed at 45° N–125° W.
[2] Tidal Datum Quality Assurance Section, NOAA, Rockville, MD 20852.
[3] Pacific Fisheries Environmental Group, P.O. Box 831, Monterey, CA 93942.

(1988). However, for years not available from Strub and James, it was estimated from weekly upwelling indices (at 45°N 125°W, Bakun, 1975; Mason and Bakun, 1986). In the latter case the time of spring transition was assigned to the first week of the year in which the weekly upwelling index became positive and remained positive for at least another week. The spring transition dates reported by Strub and James (1988) were highly correlated with our estimates (r=0.80; P<0.01). Because March is usually a month of predominant onshore Ekman transport prior to the spring transition (i.e. negative offshore Ekman transport), we determined whether YCS variation was correlated with mean onshore Ekman transport during March.

Analytical methods

Spearman's correlation analyses (Tate and Clelland, 1957) were used to account for linear and nonlinear monotonic associations between YCS and independent variables (i.e. potential egg production, environmental factors, and timing of the spring transition). Independent variables were lagged to the first year of life of each cohort to determine potential influences on YCS at the time year classes were born. Exploratory Spearman's correlation analyses were used for each season of the year because of the seasonality of different early life stages and environmental factors (Fig. 2, Appendix A).

Because many environmental-YCS relationships showed anomalous correlations during the 1958 El Niño, one of the largest El Niño events in the twentieth century (Cannon et al., 1985), this year was not included in Spearman's correlation analyses. However, after the most consistent Spearman's correlations for 1959–77 were established, all years from 1958 to 1977 were considered in regression analyses. Such regressions consisted of estimated YCS on environmental anomalies. These anomalies were computed as the actual seasonal value of a given factor minus its long-term mean for 1958–77. The use of anomalies as independent variables was justified to reduce multicollinearity effects in polynomial regressions (Neter et al., 1989).

The Bonferroni correction and the P-value plot of Schweder and Spjotvoll (1982) required individual P-values ≈0.001 for an overall P-value = 0.05 in multiple comparisons between YCS and environmental factors. Since such P-values would have made it difficult to detect meaningful ecological relationships, significance of correlations was based on individual P-values ≤0.05. Although statistical significance in our study was based on nonfiltered data (here after referred to as original series), unrelated trends in original series often cause spurious correlations and conceal the extent of year-to-year associations (Dickey et al., 1986; Norton[7]; Cohen et al., 1991). Therefore, first-order differencing was used to evaluate the reliability of correlations based on the original series (Chatfield, 1989; here after referred to as filtered series). By this criterion, a significant correlation for original series was deemed reliable only if the attendant correlation for the filtered series had the same correlation sign and a minimum absolute value ($|r| > 0.10$). Although this procedure does not account for P-values of filtered series, it provides a more consistent selection of factors potentially associated with recruitment variation.

Results

Potential spawning biomass

The effect of spawning biomass on subsequent recruitment strength was minimal as indicated by similar variations from 1970 to 1977 in YCS per parental egg and the YCS index (Fig. 3). The initial decline in YCS in the 1970's was not linked to a de-

[7] Norton, J. 1990. Relationship between California Current temperatures and intensity of the Aleutian Low. Southwest Fisheries Science Center. Report of activities. March–April 1990. La Jolla, CA, p. 16–18.

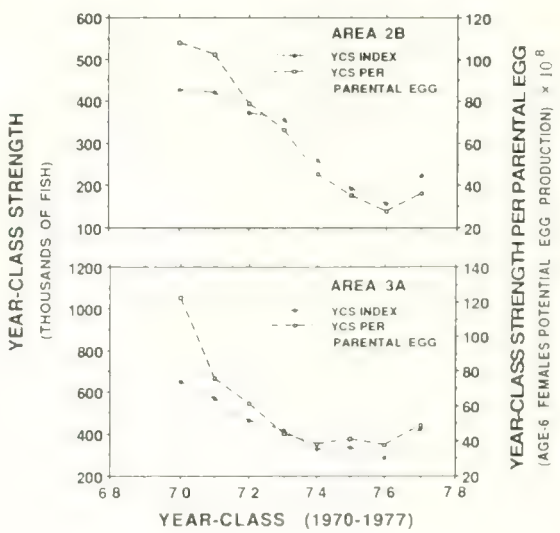

Figure 3

Comparison between year-class strength indices of petrale sole, *Eopsetta jordani*, with the attendant number of fish reaching age 6 per parental egg in Pacific States Marine Fisheries Commission areas 2B and 3A. (Cohorts considered in year-class strength indices were hatched between 1970 and 1977.)

crease in parental-stock size, as negative trends between YCS and potential egg production were observed for year classes from 1970 to 1977 (Area 2B: r=–0.81, P<0.05; Area 3A: r=–0.57, P<0.20; Fig. 4A). Examination of the attendant filtered series did not support a density-dependent relationship when the size of the parental stock was large (e.g. Ricker, 1954; Area 2B: r=0.21, Area 3A: r=0.07; Fig. 4B).

Environmental-YCS fluctuations (1959–1977)

Alongshore transport indices

1 Mean sea level height The strongest northward and southward coastal flow generally coincide with the highest and lowest mean sea levels off Oregon (Huyer et al., 1975). Long-term seasonal sea levels indicated that stronger northward and southward flows from 1959 to 1977 occurred in winter and summer, respectively (Appendix A). Correlations between YCS and mean sea level were highest in winter for both study areas (Fig. 5A). The attendant filtered series showed lower but consistent correlations for winter (Fig. 6A). Thus, recruitment strength of petrale sole seems to be associated with interannual variation in nearshore northward transport during winter.

2 Northward Ekman transport This index indicates the alongshore flow of surface mixed layers driven by wind stress. Unlike sea level height, there was no correlation between northward Ekman transport and YCS (Figs. 5B and 6B). The four long-term seasonal means of this index indicated predominantly negative northward transport (i.e. southward transport) of surface waters at offshore areas (45°N–125°W, Appendix A).

3 Northward Sverdrup transport This index measures alongshore transport over the entire water column by adding geostrophic flow to Ekman transport. For nonwinter seasons, the long-term seasonal means of this index showed southward transport of offshore waters (45°N–125°W, Appendix A). Northward Sverdrup transport and YCS were not consistently correlated (Figs. 5C and 6C).

Offshore Ekman transport The long-term seasonal means of this index indicated average offshore transport of surface waters and upwelling from spring to summer followed by onshore transport and downwelling from fall to winter (Appendix A). Winter offshore Ekman transport and YCS showed clear and consistent negative correlations in both study areas (Figs. 5D and 6D).

Cube of wind speed This index reflects the turbulence transferred to the sea surface by the wind (Niiler and Kraus, 1977). Although cube of wind speed was correlated with YCS for winter and spring (Figs. 5E and 6E), these correlations were largely explained by onshore Ekman transport during this period. Moreover, correlations for spring vanished in both areas when March was excluded from the analyses. Thus, cube of wind speed seems to be spuriously correlated with YCS.

Sea surface temperature Long-term seasonal means of sea surface temperature increased from winter through summer and decreased from fall through winter (Appendix A). Correlations between YCS and sea surface temperatures for winter and spring showed high positive

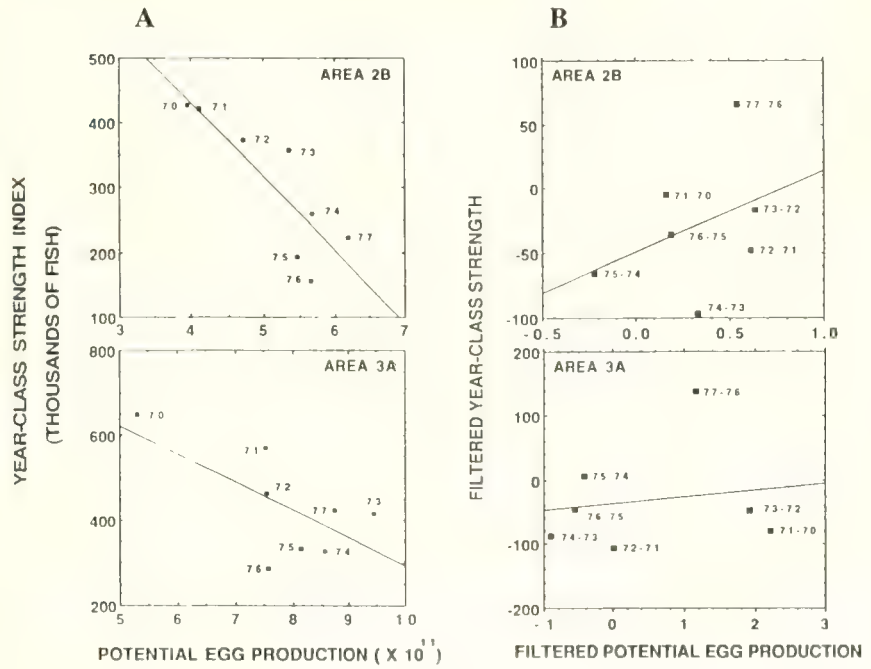

Figure 4

Variation of year-class strength of petrale sole, *Eopsetta jordani*, in relation to potential parental egg production in Pacific States Marine Fisheries Commission areas 2B and 3A. Comparison is shown for (**A**) original and (**B**) filtered series. Cohorts hatched between 1970 and 1977 (years are identified by the last two digits).

values only in Area 3A, particularly during winter (Figs. 5F and 6F). Therefore, warmer temperatures may result in increased survival of eggs and/or larvae of petrale sole in Area 3A.

Nearshore salinity index This index reflects nearshore salinity variations caused by the Columbia River plume. Although high correlations between filtered YCS and the salinity index were detected for winter and summer, no significant correlations were observed for original series (Figs. 5G and 6G).

Sea surface atmospheric pressure Nearshore transport and water properties such as temperature, salinity and density are greatly influenced by the North

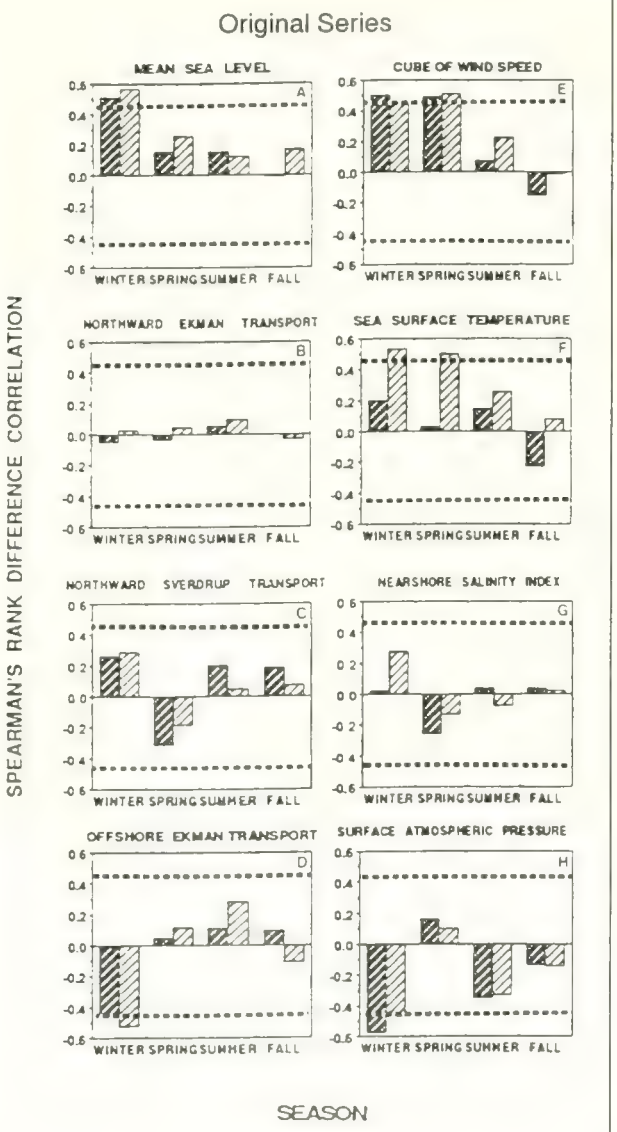

Figure 5

Spearman's correlations between year-class strength indices of petrale sole, *Eopsetta jordani*, and seasonal averages of environmental factors lagged to the first year of life (Table 2). Correlation for cohorts 1959 to 1977 are compared for Pacific States Marine Fisheries Commission areas 2B (dark bar) and 3A (light bar). Dashed lines correspond to $P = 0.05$ for individual correlations.

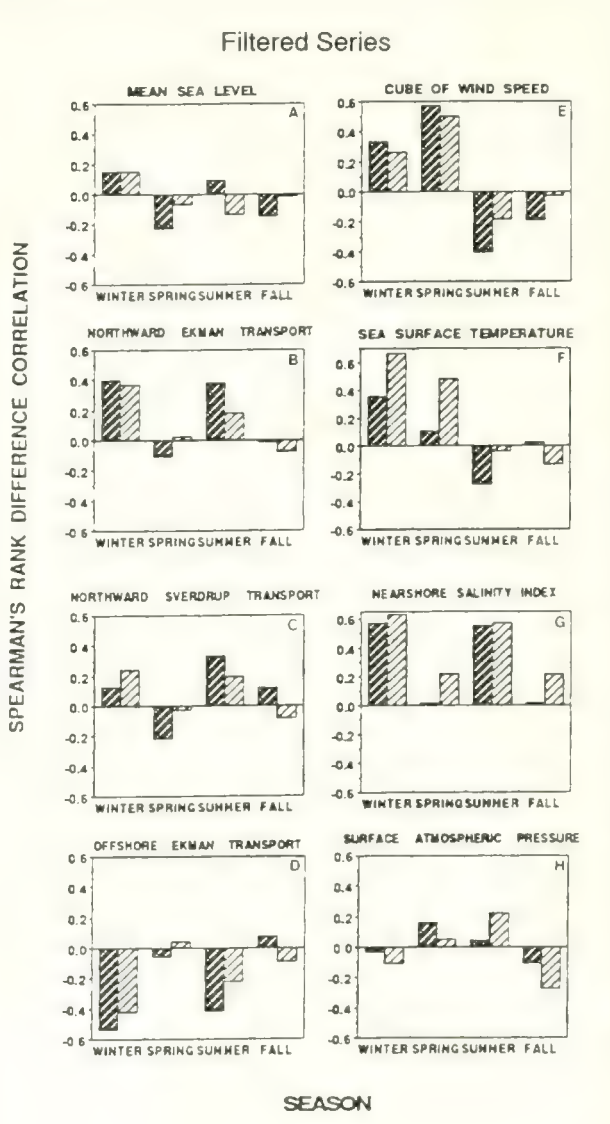

Figure 6

Spearman's correlations between filtered year-class strength indices of petrale sole, *Eopsetta jordani*, and filtered seasonal averages of environmental factors lagged to the first year of life for cohorts from 1959 to 1977 (Table 2). Areas compared are Pacific States Marine Fisheries Commission 2B (dark bar) and 3A (light bar). Significance of correlations was based on original series (see analytical methods).

Pacific high and Aleutian low pressure systems (Huyer, 1983). Large negative correlations between YCS and winter sea surface atmospheric pressure were evident in both areas (Fig. 5H). However, filtered series suggested that this index was spuriously correlated with recruitment strength (Fig. 6H).

Effects of the spring transition on YCS Correlations between YCS and the week of the spring transition from 1967 to 1977 were not significant (Area 2B: r=0.27, Area 3A: r=0.22; P>0.20; Fig. 7A). Moreover, correlations for attendant filtered series were negative (Area 2B: r=–0.18, Area 3A: r=–0.32; Fig. 7B). However, onshore transport during early spring can affect YCS as recruitment strength was correlated with mean onshore Ekman transport during March in both study areas (Area 2B: r=0.55, Area 3A: r=0.50; P<0.05). Such correlations were also supported by the attendant filtered series (Area 2B: r=0.58, Area 3B: r=0.42).

Environmental-YCS series Based on exploratory correlation analyses for original and filtered series, winter offshore Ekman transport seemed to be the main factor affecting YCS of petrale sole in areas 2B and 3A. In subsequent analyses, the period January–March was chosen for describing the association between YCS and offshore/onshore Ekman transport. This period was selected because of the importance of onshore transport on YCS during March. Moreover, correlations between offshore Ekman transport and YCS tended to be higher during January–March (original and filtered series respectively: Area 2B, r=–0.48 and –0.67; Area 3A: r=–0.52 and –0.65; P<0.05) than December–February (original and filtered series respectively: Area 2B, r=–0.46 and –0.53; Area 3A: r=–0.52 and –0.42; P≤0.05).

Comparing onshore Ekman transport with YCS, we found that two periods of reduced onshore Ekman transport (1962–65 and 1974–77) coincided with weak year classes of petrale sole (Fig. 8). The years 1958, 1961, and 1968 showed the largest positive anomalies in onshore Ekman transport from 1958 to 1977. However, unlike 1961 and 1968, the 1958 El Niño produced weak YCS in Area 2B and near-average YCS in Area 3A. Other anomalies for indices such as winter and spring sea surface temperature and winter sea level height showed some correspondence with YCS anomalies in Area 3A. In Area 2B, only onshore Ekman transport and sea level height suggested some association with YCS (Figs. 8 and 9).

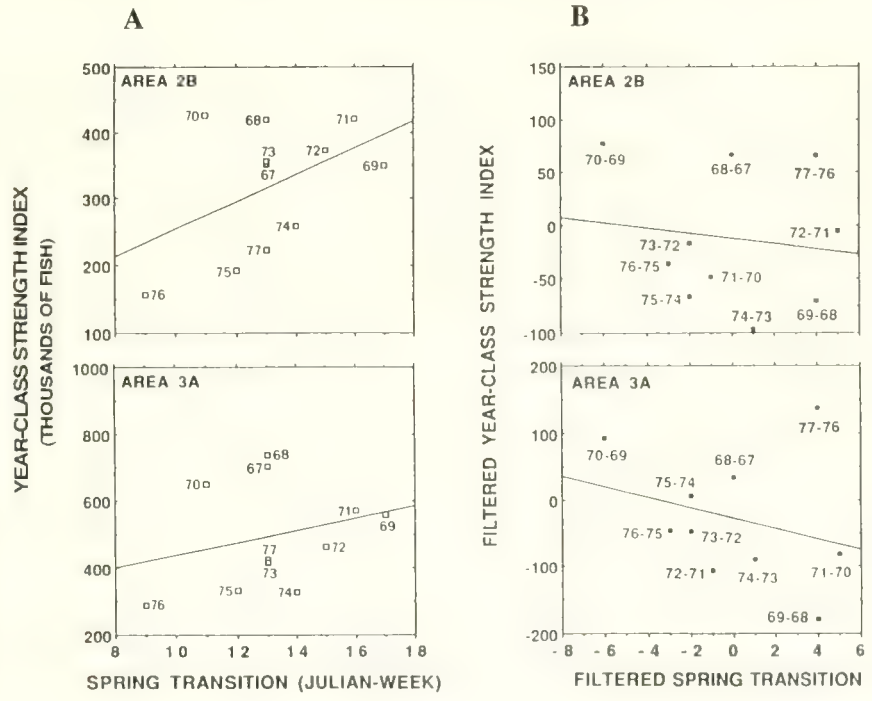

Figure 7

Variation of year-class strength for petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A in relation to the week of the year in which the spring transition occurred. Comparison is shown for (**A**) original and (**B**) filtered series. Year classes are considered hatched between 1967 and 1977 and are identified by the last two digits.

Percentage of YCS variation explained by environmental factors The relationship between YCS and January–March offshore Ekman transport anomalies was best described by second-order polynomial regressions (Fig. 10, Table 3). Associations between YCS and winter sea level height anomalies in areas 2B and 3A, were also described by second-order polynomials (Fig. 11, Table 3). Although the association between YCS and winter sea surface temperature in Area 3A was better described by a second-order polynomial than by a linear regression, only the latter was significant (Fig. 12, Table 3). Except for the year 1958, and for the years with large anomalies in offshore Ekman transport

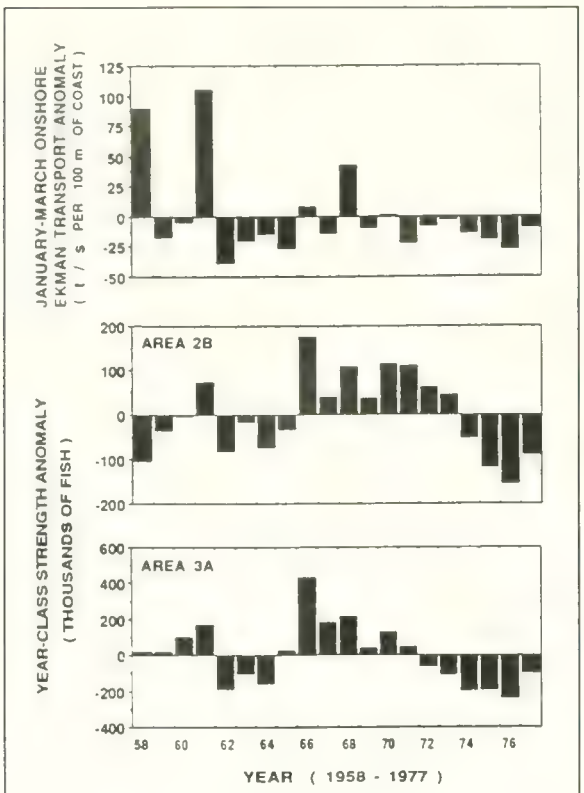

Figure 8

Anomalies for mean onshore Ekman transport off Oregon (January to March), and for year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A. (Values computed from the long-term mean 1958–77.)

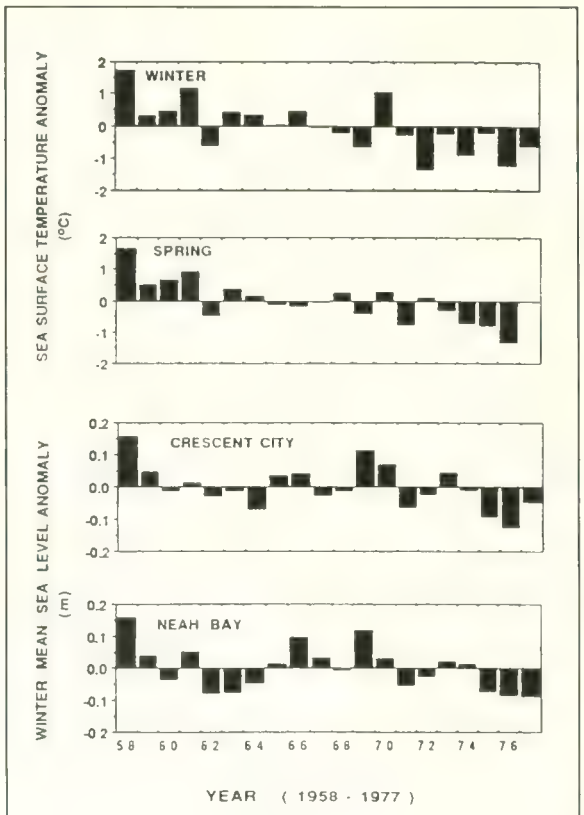

Figure 9

Anomalies of sea level height (Crescent City and Neah Bay), and winter and spring sea surface temperature off Oregon-Washington (considered for Area 3A). Values based on the long-term mean 1958–77. (Locations for environmental indices are shown in Table 2.)

(i.e. 1961, 1968; Fig. 10) and sea level height (i.e. 1969; Fig. 11), a common feature in these regressions is the nearly linear association for most of the studied period.

Regressions for individual environmental factors explained less than 40% of the YCS variation in each area from 1958 to 1977 (Table 3). However, a regression model including offshore Ekman transport and sea level height accounted for nearly 55% of the YCS in Area 2B (Fig. 13). Over the same period in Area 3A, these two environmental factors plus sea surface temperature explained about 65% of the variation in YCS.

Discussion

Recruitment variation of petrale sole in areas 2B and 3A was correlated with oceanographic conditions from winter to early spring, the period in which egg and larval stages of this species are most abundant. Since postsettlement, age-0 petrale sole have only been found within the inner continental shelf (Ketchen and Forrester, 1966; Gregory and Jow, 1976; Pearcy et al., 1977), and YCS and offshore Ekman transport were consistently and negatively correlated, it is possible that inshore advection of eggs and larvae toward nearshore settlement areas may be the major factor determining YCS in this species.

A critical assumption for establishing spawner-recruit relationships is that density-independent survival variation at early life stages is negligible when compared with variation in spawning biomass. This assumption is not consistent with the results obtained in our study, with the lack of spawner-recruit relationships for petrale sole in other areas (Ketchen and Forrester, 1966), and with the results of most flatfish studies (Cushing, 1971; Roff, 1981).

Our findings support the hypothesis that recruitment of petrale sole is dependent on northeastward

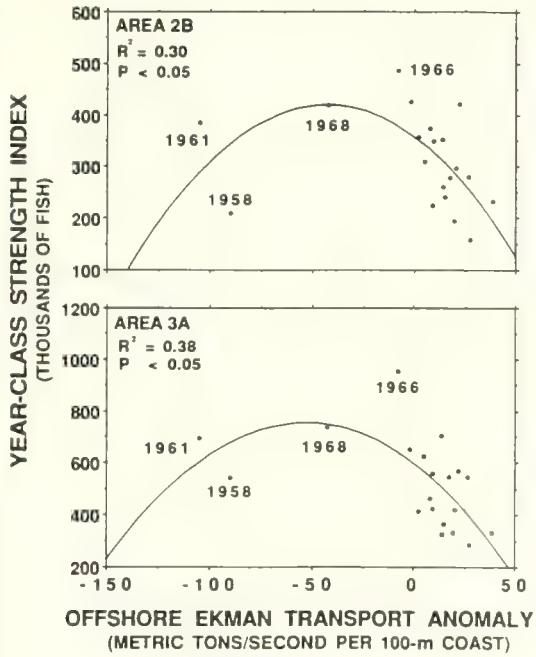

Figure 10

Relations between year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A and mean offshore Ekman transport anomaly off Oregon from January to March. (Regression parameters are shown in Table 3.)

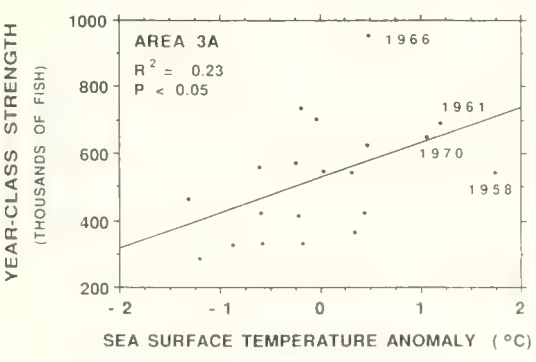

Figure 12

Relation between year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission Area 3A and mean winter sea surface temperature anomaly off Oregon-Washington (December-February). (Regression parameters are shown in Table 3.)

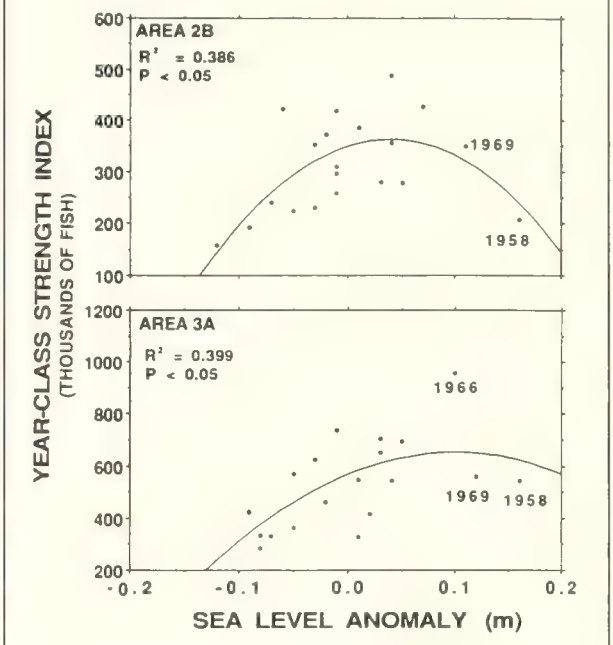

Figure 11

Relations between year-class strength of petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A and winter mean sea level height anomalies. (Regression parameters are shown in Table 3.)

transport during winter (Ketchen and Forrester, 1966). The analyses in Area 3A are also consistent with an association between temperature and survival of early life stages of petrale sole (Ketchen and Forrester, 1966; Alderdice and Forrester, 1971). Considering the discharge of the Columbia River into Area 3A and the stenohaline condition of eggs and larvae in this species, possible salinity-YCS associations may be overridden by cross-shore and alongshore advection and sea temperature.

Recruitment strength of petrale sole was correlated between areas 2B and 3A (r=0.82, P<0.01). However, the highest determination coefficient for regression models of YCS on environmental factors was obtained in Area 3A. Although the proportion of variation in YCS explained by second-order polynomial regressions was significant for both offshore Ekman transport and sea level height, filtered series suggest that year-to-year variation in YCS were better explained by the former. Unlike Area 3A and off British Columbia (Ketchen and Forrester, 1966), no regression models of YCS on sea surface temperature were significant or marginally significant in Area 2B. The higher positive temperature-YCS association for Area 3A compared with Area 2B is consistent with temperature differences between areas (Appendix A). These observations suggest a latitudinal effect of temperature on the recruitment of petrale sole, that is, higher recruitment toward the poleward range of the

Table 3

Regressions of year-class strength (YCS) for petrale sole, *Eopsetta jordani* (thousands of females attaining age 6), on environmental anomalies in Pacific States Marine Fisheries Commission areas 2B and 3A from 1958 to 1977. Environmental anomalies are based on the long-term mean 1958–77. SST = sea surface temperature anomaly (Dec.–Feb.), SL = mean sea level height anomaly (Dec.–Feb.), Me = offshore Ekman transport anomaly (Jan.–Mar.). $P \leq 0.05$ for significant correlations (n = 20 years). In the last regression model, R^2 = 0.667 between predicted YCS ($e^{\ln(YCS)}$) and YCS index ($P<0.05$).

Area	Regression model	R^2	P
	YCS on SST		
3A	YCS = 524.5048 + 104.8226 SST	0.231	<0.05
	YCS on SST and SST^2		
3A	YCS = 550.4459 + 116.8338 SST – 44.9699 SST^2	0.270	0.06*
	YCS on Me and Me^2		
2B	YCS = 357.0224 – 2.9121 Me – 0.0340 Me^2	0.302	<0.05
3A	YCS = 576.0152 – 4.3035 Me – 0.0391 Me^2	0.381	<0.05
	YCS on SL and SL^2		
2B	YCS = 347.0157 + 625.3314 SL – 8103.1487 SL^2	0.386	<0.05
3A	YCS = 565.1595 + 1686.4019 SL – 8512.4524 SL^2	0.399	<0.05
	YCS on Me, Me^2, SL and SL^2		
2B	YCS = 377.9325 – 2.3712 Me – 0.0255 Me^2 + 346.4281 SL –7477.8599 SL^2	0.549	<0.05
3A	YCS = 608.3490 – 3.8546 Me – 0.0378 Me^2 + 1104.2691 SL –7115.5843 SL^2	0.508	<0.05
	Ln (YCS) on Me, Me^2, SL, SL^2, SST and SST^2		
3A	Ln (YCS) = 6.4115 – 0.0068 Me – 6×10–5 Me^2 + 1.9585 SL –9.0066 SL^2 + 0.1069 SST – 0.1321 SST^2	0.648	<0.05

* Nonsignificant.

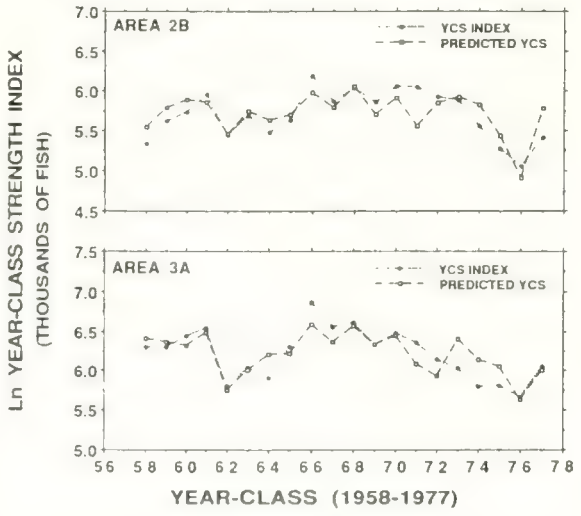

Figure 13

Log-transformed estimated and predicted year-class strength for petrale sole, *Eopsetta jordani*, in Pacific States Marine Fisheries Commission areas 2B and 3A. Area 2B: prediction is based on anomalies of offshore Ekman transport and sea level height and their attendant squared values. Area 3A: predicted values are based on anomalies of offshore Ekman transport, sea level height, sea surface temperature, and their attendant squared values. (Regression parameters are shown in Table 3.)

species' distribution in warmer years (Cushing, 1982; Bailey and Incze, 1985; Frank, 1991).

The interrelation among oceanographic factors (e.g. Huyer, 1977; Kruse and Huyer, 1983) makes it difficult to determine the importance of any single environmental factor to YCS variation. Hence, the more consistent negative correlation between YCS and offshore Ekman transport in Area 3A than in Area 2B could be due in part to a higher correlation between YCS and sea surface temperature in Area 3A.

Primary production and usable solar radiation seem to be positively correlated during winter and spring off Oregon (Small et al., 1972). However, no associations between YCS of petrale sole and mean usable radiation were observed from solar radiation estimates for winter or spring near areas 2B[8] and 3A[9] (Castillo, unpubl. data). On the other hand, although a nearly tenfold increase in zooplankton production from winter to summer may be stimulated by coastal upwelling off Oregon (Peterson and Miller, 1977), correlations between YCS of petrale sole and spring or summer upwelling indices did not suggest that recruitment strength is primarily controlled by

[8] U.S. Weather Bureau. 1961–1964. Local climatological data, Medford, Municipal Airport, Oregon, U.S. Dep. Commerce. USCOMM-WB-Asheville.

[9] U.S. Weather Bureau. 1958–1964. Local climatological data, Clatsop County Airport, Astoria, Oregon, U.S. Dep. Commerce. USCOMM-WB-Asheville.

zooplankton production. Such inference is consistent with observations for two other species of flatfish in Area 3A (Hayman and Tyler, 1980).

Years of strong cohorts of petrale sole and other flatfishes tended to co-occur off Oregon during the 1960's (e.g. 1961, 1966, and 1968).[10] Year class 1961 was strong for nearly 85% of 13 groundfish species from the Northeast Pacific (Hollowed et al., 1987). The high onshore Ekman transport in winter 1961 (Fig. 10) suggests that major factors controlling YCS in petrale sole are the same for other groundfish species.

Acknowledgments

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Literature Cited

Alderdice, D. F., and C. R. Forrester.
1971. Effects of salinity and temperature on embryonic development of the petrale sole (*Eopsetta jordani*). J. Fish. Res. Board Can. 28:727–744.

Bailey, K. M., and L. S. Incze.
1985. El Niño and the early life history and recruitment of fishes in temperate marine waters. *In* W. S. Wooster and D. L. Fluharty (eds.), El Niño North, p. 143–165. Wash. Sea Grant Progr. Univ. Wash., Seattle.

Bakun, A.
1973. Coastal upwelling indices, west coast of North America, 1946–71. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671, 103 p.
1975. Daily and weekly upwelling indices, west coast of North America. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-693, 114 p.

Best, E. A.
1963. Movements of petrale sole, *Eopsetta jordani* (Lockington) tagged off California. Pac. Mar. Fish. Comm. Bull. 6:24–38.

Botsford, L. W., D. A. Armstrong, and J. M. Shenker.
1989. Oceanographic influences on the dynamics of commercially exploited populations. *In* M. R. Landry and B. M. Hickey (eds.), Coastal oceanography of Washington and Oregon, p. 511–563. Elsevier Oceanogr. Ser. 47.

Cannon, G. A., R. K. Reed, and P. E. Pullen.
1985. Comparison of El Niño events off the Pacific Northwest. *In* W. S. Wooster and D. L. Fluharty (eds.), El Niño north, p. 75–84. Wash. Sea Grant Progr. Univ. Wash., Seattle.

Castillo, G. C.
1992. Fluctuations of year-class strength in petrale sole (*Eopsetta jordani*) and their relation to environmental factors. M.S. thesis, Oregon State Univ. Corvallis, OR, 99 p.

Chatfield, C.
1989. The analysis of time series, 4th ed. Chapman and Hall, G.B., 241 p.

Cleaver, F. C.
1949. The Washington otter trawl fishery with reference to the petrale sole (*Eopsetta jordani*). Wash. Dep. Fish., Biol. Rep. 49A:1–45.

Cohen, E. B., D. G. Mountain, and R. O'Boyle.
1991. Local-scale versus large-scale factors affecting recruitment. Can. J. Fish. Aquat. Sci. 48: 1003–1006.

Cushing, D. H.
1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. int. Explor. Mer 33:340–362.
1982. Climate and fisheries. Academic Press, London, 373 p.

Dickey, D. A., W. R. Bell, and R. B. Miller.
1986. Unit roots in time series models: tests and implications. Am. Stat. 40:12–26.

DiDonato, G. S., and N. Pasquale.
1970. Migration of petrale sole tagged in deep water off the Washington coast. Wash. Dep. Fish. Res. Pap. 3:53–61.

Frank, K. T.
1991. Predicting recruitment variation from year-class specific vertebral counts: an analysis of the potential and a plan for verification. Can. J. Fish. Aquat. Sci. 48:1350-1357.

Gregory, P. A., and T. Jow.
1976. The validity of otoliths as indicators of age of petrale sole from California. Calif. Fish Game 62:132–140.

Halpern, D.
1976. Structure of a coastal upwelling event observed off Oregon during July 1973. Deep-Sea Res. 23:495–508.

Harry, G. Y.
1959. Time of spawning, length at maturity, and fecundity of the English, petrale and Dover soles (*Parophrys vetulus*, *Eopsetta jordani*, and *Microstomus pacificus*, respectively). Oreg. Fish Comm. Res. Briefs 7:5–13.

Hayman, R. A., and A. V. Tyler.
1980. Environmental and cohort strength of Dover sole and English sole. Trans. Am. Fish. Soc. 109:54–70.

[10] Demory, R. L., M. J. Hosie, N. T. Eyck, and B. O. Forsberg. 1976. Groundfish surveys on the continental shelf off Oregon, 1971–74. Oregon Department of Fish and Wildlife Information Rep. 76-9.

Hayman, R. A., A. V. Tyler, and R. L. Demory.
1980. A comparison of cohort analysis and catch per unit effort for Dover sole and English sole. Trans. Am. Fish. Soc. 109:35–53.

Hitz, C. R., and W. F. Rathjen.
1965. Bottom trawling surveys of the northeastern Gulf of Alaska. Commer. Fish. Review 27:1–15.

Hollowed, A. B., K. M. Bailey, and W. S. Wooster.
1987. Patterns of recruitment of marine fishes in the Northeast Pacific Ocean. Biol. Oceanogr. 5:99–131.

Huyer, A.
1977. Seasonal variation in temperature, salinity, and density over the continental shelf off Oregon. Limnol. Oceanogr. 22:442–453.
1983. Coastal upwelling in the California Current System. Progr. Oceanogr. 12:259–284.

Huyer, A., R. D. Pillsbury, and R. L. Smith.
1975. Seasonal variation of the alongshore velocity field over the continental shelf off Oregon. Limnol. Oceanogr. 20:90–95.

Jones, R.
1981. Analysis of age composition data. *In* The use of length composition data in fish stock assessment (with notes on VPA and cohort analysis), p. 1–17. FAO Fish. Circ. 734.

Ketchen, K. S.
1956. Climatic trends and fluctuations in yield of marine fisheries of the Northeast Pacific. J. Fish. Res. Board Can. 13:357–374.

Ketchen, K. S., and C. R. Forrester.
1966. Population dynamics of the petrale sole, *Eopsetta jordani*, in waters off western Canada. Fish. Res. Board Can. Bull. 153, 195 p.

Kruse, G. H., and A. Huyer.
1983. Relationships among shelf temperatures, coastal sea level, and the coastal upwelling index off Newport, Oregon. Can. J. Fish. Aquat. Sci. 40:238–242.

Landry, M. R., J. R. Postel, W. K. Peterson, and J. Newman.
1989. Broad-scale distributional patterns of hydrographic variables on the Washington/Oregon shelf. *In* M. R. Landry and B. M. Hickey (eds.), Coastal oceanography of Washington and Oregon, p. 1–40. Elsevier Oceanogr. Ser. 47.

Mason, J. E., and A. Bakun.
1986. Upwelling index update, U.S. west coast, 33°N–48°N latitude. NOAA-TM-NMFS-SWFC-67, 81 p.

Nelson, C. S.
1977. Wind stress and wind stress curl over the California Current. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-714, 87 p.

Neter, J., W. Wasserman, and M. H. Kutner.
1989. Applied linear regression models, 2nd ed. Donneley & Sons Co., 667 p.

Niiler, P. P., and E. B. Kraus.
1977. One-dimensional models in the upper ocean. *In* E. B. Kraus (ed.), Modelling and prediction of the upper layers of the ocean, p. 143–172. Pergamon Press, England.

Parrish, R. H., C. S. Nelson, and A. Bakun.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.

Pearcy, W. G., M. J. Hosie, and S. L. Richardson.
1977. Distribution and duration of pelagic life of larvae of Dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; and petrale sole, *Eopsetta jordani*, in waters off Oregon. Fish. Bull. 75:173–183.

Pedersen, M. G.
1975. Movements and growth of petrale sole (*Eopsetta jordani*) tagged off Washington and southern Vancouver Island. J. Fish. Res. Board Can. 32:2169–2177.

Peterson, W. T., and C. B. Miller.
1977. Seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. Fish. Bull. 75:717–724.

Porter, P.
1964. Notes on fecundity, spawning and early life history of petrale sole (*Eopsetta jordani*), with descriptions of flatfish larvae collected in the Pacific Ocean off Humboldt Bay, California. M.S. thesis, Humboldt State College, 98 p.

Ricker, W. E.
1954. Stock and recruitment. J. Fish. Res. Board Can. 11:559–623.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Roedel, P. M.
1953. Common ocean fishes of the California coast. Calif. Dep. Fish Game, Fish Bull. 91, 184 p.

Roff, D. K.
1981. Reproductive uncertainty and the evolution of iteroparity: Why don't flatfish put all their eggs in one basket? Can. J. Fish. Aquat. Sci. 38:968–977.

Rothschild, B. J., and C. G. Rooth.
1982. Fish ecology III. A foundation for REX, a recruitment experiment. Univ. Miami. Tech. Rep. 82008, 388 p.

Schweder, T., and E. Spjotvoll.
1982. Plots of *P*-values to evaluate many tests simultaneously. Biometrika 69:493–502.

Shepherd, J. G., J. G. Pope, and R. D. Cousens.
1984. Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-v. Reun. Cons. int. Explor. Mer 185:255–267.

Sissenwine, M. P.
1984. Why do fish populations vary? *In* R. M. May (ed.), Exploitation of marine communities, p. 59–94. Springer-Verlag, Berlin.

Small, L. F., H. Curl, and W. A. Glooschenko.
1972. Effects of solar radiation and upwelling on daily primary production off Oregon. J. Fish. Res. Board Can. 29:1269–1275.

Smith, P. E.
1981. Time series of anchovy larva and juvenile abundance. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178:201.

Strub, P. T., and C. James.
1988. Atmospheric conditions during the spring and fall transitions in the coastal ocean off western United States. J. Geophys. Res. 93: 15561–15584.

Strub, P. T., J. S. Allen, A. Huyer, and R. L. Smith.
1987. Large-scale structure of the spring transition in the coastal ocean off western North America. J. Geophys. Res. 92:1527–1544.

Tate, M. W., and R. C. Clelland.
1957. Nonparametric and shortcut statistics in the social, biological and medical sciences. Interstate Printers and Publishers, Inc., Danville, IL, 171 p.

Appendix A

Long-term seasonal means (1959–77) of environmental indices used in exploratory correlation analyses. Except for mean sea level height and sea surface temperature, only one index per environmental factor was considered for Pacific States Marine Fisheries Commission areas 2B and 3A. (Geographical locations and sources for environmental indices are shown in Table 2.)

	Environmental indices									
	Mean sea level height[1]		Northward Ekman tran.[2]	Northward Sverdrup tran.[3]	Offshore Ekman tran.[4]	Cube of wind speed[5]	Sea surface temperature[6]		Nearshore salinity index[7]	Sea surface atmos. pressure[8]
Season	Area 2B	Area 3A					Area 2B	Area 3A		
Winter	2.09	2.33	– 26.09	18.43	– 72.31	155.16	10.40	9.38	9984.63	1017.60
Spring	1.93	2.19	– 20.02	– 117.43	9.97	46.17	10.73	10.16	9990.12	1018.65
Summer	1.88	2.25	– 14.24	– 200.35	61.28	104.99	13.67	13.85	10102.03	1018.58
Fall	1.98	2.29	– 10.69	– 15.63	– 19.71	53.31	13.22	12.87	9999.48	1017.17

[1] Meters.
[2] Value × 10 = metric tons per second per kilometer.
[3] Value × 100 = metric tons per second per kilometer.
[4] Metric tons per second per 100 meter of coast width
[5] (meters/second)^3.
[6] Value = Celsius degrees.
[7] Value/10,000=water density (grams/cm^3) at 15°C.
[8] Millibars.

The distribution, food, and age of juvenile bluefish, *Pomatomus saltatrix*, in Maine

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Abstract.—The bluefish, *Pomatomus saltatrix* (Linnaeus), is abundant in the South and Middle Atlantic Bights, where more than 75% of the shore-based catches are juveniles (age 0). No information is available on the distribution, food, and age of juvenile bluefish north of the Middle Atlantic Bight. The objectives of the present study were to review and summarize unpublished records of catch locations, to characterize the diet of juvenile bluefish, and to derive parent spawning dates (and possible spawning locations) for juvenile bluefish in Maine. Most observations of juvenile bluefish were from southwestern Maine. The most northeasterly site was Little Kennebec Bay (near Machiasport, Maine). During this study, juvenile bluefish were collected from three locations: Marsh River (1990–1991), Sagadahoc Bay (1990), and Merepoint Bay (1991). The diet of juvenile bluefish varied with size. Fish from Sagadahoc Bay, measuring 37–64 mm fork length (FL), fed predominantly on mysids and copepods. Fish from the Marsh River, measuring 81–200 mm FL, fed on fish and large crustaceans. Daily growth rings were counted on the sagitta of juvenile bluefish. Spawning dates, backcalculated from these counts, suggest that fish captured in the Marsh River (1990–1991) originated from a spring spawning (March–May), and fish captured in Sagadahoc Bay (1990) originated from a summer spawning (predominantly June). We do not believe that these spring and summer spawned fish originated from the known major spring and summer spawning grounds in the South and Mid-Atlantic Bights, respectively. The time required to swim from even the northern portion of these major spawning grounds to the site of capture exceeds the known age of the fish derived from counting daily growth rings. The results suggest that both major spawning areas have been extended to the northeast, or unknown spawning areas exist closer to Maine.

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Fishery Bulletin 92:494–508 (1994).

Bluefish, *Pomatomus saltatrix*, are widely and irregularly distributed along the continental shelf in temperate and warm water regions (Briggs, 1960; Wilk, 1977). On the Atlantic coast of North America the species is particularly abundant in southern Florida, North Carolina, Virginia, and from New Jersey to southern Massachusetts, where it is highly sought by salt water recreational anglers for its superior fighting qualities. Stray adult bluefish have been reported during the summer in New Brunswick waters (Bay of Fundy, Passamaquoddy Bay, St. Johns River) and the south shore of Nova Scotia (Scott and Scott, 1988). In the Gulf of Maine, the abundance of bluefish has fluctuated widely over time (Bigelow and Schroeder, 1953). During the mid-1970's, an increase in abundance resulted in the development of a major recreational fishery for adult fish in Maine. This increase is reflected in the incidental bluefish catch recorded since 1986 from gillnet fishing activity for more desirable commercial species (cod, etc.): 46.9 metric tons (t) (1986); 8.8 t (1987); 3.9 t (1988); 34.6 t (1989); 24.4 t (1990); 51.9 t (1991); 37.0 t (1992).[1]

Both shore and boat-based recreational fisheries exploit young bluefish (age 0 and 1) in the South Atlantic. More than 75% of the shore-based recreational catch along the south and mid-Atlantic coasts are juvenile fish (age 0).[2] Although isolated reports of juvenile bluefish have been reported in Maine waters (Bigelow and Schroeder, 1953; Lund, 1961; Targett and McCleave, 1974), no information is available on the distribution, food, and age of these fish. The objectives of this study were 1) to review and summarize unpublished locations where juvenile bluefish have been captured between the Piscataqua River (Maine-New Hampshire border) and Passamaquoddy Bay (Maine-New Brunswick border), 2) to characterize the diet of juvenile bluefish in Maine, and 3) to derive parent spawning dates and possible spawning locations from counts of daily growth rings on juvenile bluefish otoliths obtained in Maine.

Materials and methods

Records of juvenile bluefish in Maine

Unpublished records of juvenile bluefish along coastal Maine were reviewed. Sightings were considered reliable if we actually observed the specimens of juvenile bluefish reported or if the observers could

[1] Morrill, R. NMFS Port Agent, Portland, Maine. Personal commun., 1993.

[2] Crecco, V., M. Terceiro, and C. Moore. 1987. A stock assessment of Atlantic coast bluefish, *Pomatomus saltatrix*. Special report prepared for the Atlantic States Marine Fisheries Commission, Washington, D.C., 86 p.

correctly identify preserved juvenile bluefish from the laboratory fish collection.

Study locations

The primary sampling sites were in the Marsh River (a tributary of the Sheepscot River in Newcastle, Maine) near the confluence of Sherman Lake Outlet and Deer Meadow Brook (Fig. 1A). These sites were selected because juvenile bluefish were consistently captured there in preliminary netting experiments conducted during the summers of 1986–89. The sites are approximately 6.5 km from the confluence of the Marsh River and the Sheepscot River and 34.3 km from the mouth of the Sheepscot River. Marsh banks abut the meandering river and mud flats slope from the base of these banks to the edge of the riverbed. The riverbed is about 46–49 m wide at low tide. The mean tidal range is 1.60 m (U.S. Dep. Commer., 1990–91).

Juvenile bluefish were also obtained from sampling sites at Kennebec Point (Fig. 1B) and Merepoint Bay (Fig. 1C). The Kennebec Point site is used routinely by the Division of Benthic and Demersal Fisheries (State of Maine, Dep. of Marine Resources, W. Boothbay Harbor, Maine 04575) to monitor biweekly variation in species diversity and abundance; occasionally, juvenile bluefish were captured there. The site consists of a sandy beach and a small cove, 1.8 km from open ocean. The mean tidal range is 1.37 m (U.S. Dep. Commer., 1990–91).

Abundant schools of juvenile bluefish and clupeids inhabit the Merepoint Bay site, located in shallow water between the floats at Paul's Marina (Fig. 1C). This site is 16.7 km from open ocean and the tidal range is 1.46 m (U.S. Dep. Commer., 1990–91).

Sampling gear

Gill nets were employed to capture juvenile bluefish in the Marsh River for the following reasons. First, the fish were dispersed and sporadic in occurrence and other methods of capture would probably have produced few fish. Swift tidal currents prevented the use of seines at other than low slack water, and a seine requires two operators and frequently only one was available.

Two sinking gill nets (Sterling Marine Products, Jonesport, Maine 04649), measuring 2.4 m in depth and 48.8 m in length, were suspended between stakes driven into the banks of the Marsh River. Ropes suspending these nets bifurcated 4.6 m from the end of each net; one length was attached to the float line and the other to the lead line. Poles measuring 2.1 m were positioned between the float and lead lines at each end of each net to prevent the nets from collapsing and twisting during rapid tidal flows at mid-ebb and mid-flood. A window weight (2.4 kg) was attached to the lower end of each pole to maintain the net vertically. One net was a variable mesh type constructed from two 6.1-m panels of each of the following square mesh sizes: 1.27 cm, 1.90 cm, 2.54 cm, and 3.18 cm. Individual panels were randomly positioned. Additional floats were attached to the float line of these sinking nets so they fished approximately 15–30 cm below the surface. This enabled floating debris to pass over the net. The second net was constructed entirely of 1.27-cm square mesh.

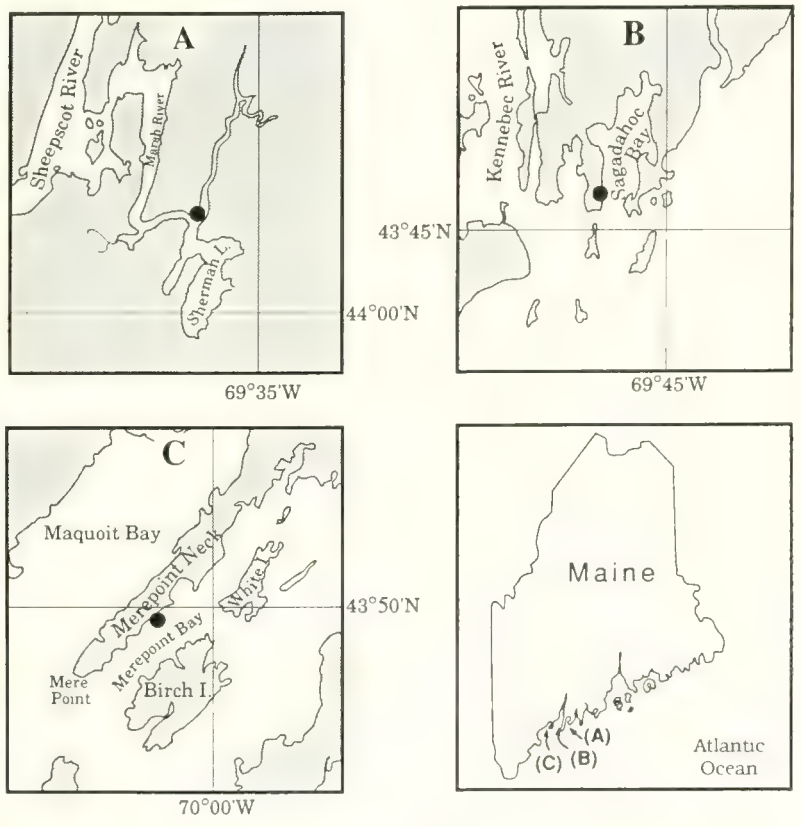

Figure 1

Sampling locations for juvenile bluefish, *Pomatomas saltatrix*, in (**A**) Marsh River, (**B**) Sagadahoc Bay, and (**C**) Merepoint Bay, Maine.

Beginning in June, gill nets were fished for approximately four hours, once a week, until catches revealed that bluefish were present in the river. The nets were then fished two or three times a week. Fishing was again reduced to one set per week in September when no further catches of bluefish were made. When two weeks of fishing produced no juvenile bluefish, fishing was discontinued. Gill nets were set in the Marsh River on 20, 27 June; 4, 11, 18, 25 July; 1, 6, 14, 16, 21, 22, 23, 27, 28, 30 August; 5, 6, 11, 12, 18, 20, 26 September; 3, 12 October 1990 and 20, 26 June; 9, 17, 22, 25, 29 July; 1, 6, 12, 15, 22, 29 August; 4, 5, 10, 12, 17 September; and 1, 8 October 1991. When bluefish were present, the net was inspected every 30 minutes without pulling and resetting it. All fish were removed from the net, identified to species, and measured to the nearest mm.

Juvenile bluefish were captured by beach seine on 10 August 1990 and 27 September 1991 at Kennebec Point. The seine was constructed of 6.35-mm square mesh and measured 1.2 m × 15.2 m. It was hauled a horizontal distance of 152.4 m on each sampling date. Fish were also collected at Kennebec Point on 22 August 1990 in a fyke net constructed of 6.35-mm square mesh with two 15.2-m wings. The fyke net was set in a dry channel at low tide, and a 3-hour set was initiated when the incoming tide first reached the hoops. Juvenile bluefish were captured at Merepoint on 9 September 1991 by using the variable mesh gill net described previously.

Field and laboratory data recorded

Fishing time was recorded during each sampling trip to the Marsh River. The set was initiated when the net was set, attached to stakes, and spread. Termination of the set occurred when the net was detached from one stake. Temperature and salinity were recorded at the surface and bottom with a YSI Model 33 SCT Meter immediately following the beginning of a set and just prior to the end of a set. Tide condition, time of slack water (if it occurred), and maximum depth noted from graduations on the SCT cable were also recorded.

Both individuals and schools (two or more gilled in close proximity) of juvenile bluefish were captured in the gill nets. The fish were stored in plastic bags containing information on time of capture (to the nearest 30 minutes), date of capture, and mesh size of the capture panel. Fish were stored in an ice cooler until returned to the laboratory.

Within nine hours of capture, fish were wiped with paper towels and weighed to the nearest 0.1 gram. Both total length (TL) and fork length (FL) (Hubbs and Lagler, 1958) were recorded to the nearest millimeter. Stomachs were removed and frozen in small scintillation vials. Heads were refrigerated until the sagitta were removed.

Daily growth rate was derived from the total increase in length divided by the number of daily growth increments counted. Total growth in length is equivalent to size (FL) at capture minus the approximate size at hatching (2 mm, Deuel et al., 1966).

Treatment and analysis of stomach contents

Stomachs were thawed and submerged in 3% sea water formalin for approximately 19 hours to harden stomach contents. Stomachs were then rinsed several times with sea water and their contents were identified to the lowest taxon, counted, blotted on a paper towel, and weighed to 0.0001 grams. Stomach contents were then refrozen and freeze-dried (Labconco Freeze Dryer 8) for 48 hours at –40°C under a vacuum of approximately 25 microns mercury (Hg). Dry weights were recorded to the nearest 0.0001 gm.

Three prey item indices were computed to reduce potential bias associated with a single index (Hynes, 1950; Windell, 1971; Friedland et al., 1988). We employed the methodology of Friedland et al. (1988) in computing 1) the number of stomachs in which a species occurred expressed as a) a percentage of the total number of stomachs containing food (F=percent frequency of occurrence) and b) a percentage of the total number of stomachs examined (F1=percent frequency of occurrence); 2) the number of individuals of each prey species expressed as a percentage of the total number of food items (N=percent numerical abundance); and 3) the wet weight of a species expressed as a percentage of the total wet weight of food items (W=percent wet weight) and the dry weight of a species expressed as a percentage of the total dry weight of food items (W1=percent dry weight).

Preparation and analysis of otoliths

Saggita were removed from each fish within 24 hours of capture. Excess tissue was removed with forceps. Pairs of sagitta were stored in 7-mL scintillation vials for 1–3 months prior to mounting and ageing. Each sagitta was mounted concave side down on a microscope slide with Epo-Kwick (Buehler Ltd., Lake Bluff, Illinois). Commercial grade wet-dry sandpaper (600 grit or 24 μ) was used for initial coarse sanding. Final sanding and polishing was performed with 9-μ and 0.3-μ wet-dry sandpaper respectively (Buehler, Ltd). The addition of a small drop of glycerine to the surface of the polished otolith assisted in the resolution of daily growth rings. Three replicate counts were performed during one day by one

reader using a compound microscope with transmitted polarized light at 100–200×. Counts were rarely accomplished in a straight line; it was usually necessary to traverse the otolith in either a general dorsal or ventral direction to complete a count because daily growth rings in many portions of the otolith are obscure. Each counting pathway was usually different. The criterion of Nyman and Conover (1988) was used: if one of three counts differed by >10%, an additional count was performed and the value that differed by >10% was discarded. The mean of the three remaining counts was recorded. Dates of first ring deposition for juvenile bluefish collected from all sources were backcalculated from the number of growth increments counted.

Estimates of swimming speed and swimming distance

The distance juvenile bluefish were capable of swimming per day was calculated from estimates of the average body length during migration and the relationship between swimming speed and average body length. Average body length was equal to one-half the mean size of fish collected during a 2-week period immediately following first appearance at a sampling site minus 2 mm, the size at hatching (Deuel et al., 1966). The swimming speed for fish such as salmon, cod, and herring is about three times the body length/sec for fish measuring 10–100 mm (Harden Jones, 1968). Juvenile bluefish measuring 155–213 mm TL swam at speeds averaging 94 mm/sec at 20°C and 180–260 mm/sec when cooler water was added (Olla et al., 1985). We estimated swimming speed of juvenile bluefish at no more than 2 body length/sec.

The mean size of juvenile bluefish collected from the Marsh River during a 2-week period immediately following their first appearance in 1990 and 1991 was 108 mm FL (n=17) and 101 mm FL (n=19). Total growth between hatching and appearance at the collection site in 1990 was 106 mm (108 mm minus 2 mm [the size at hatching]) and in 1991, 99 mm. The average size of the fish during this migration would be one-half these values or 53 and 50 mm. Swimming distances per day during migrations in 1990 and 1991 were 53 mm × 2 (twice the body length) = 106 mm/sec (9.16 km/day) and 50 mm × 2 = 100 mm/sec (8.64 km/day). Similarly, the mean size of juvenile bluefish collected from Sagadahoc Bay during August 1990 was 48 mm FL (n=29). The swimming distance per day was therefore 23 mm × 2 = 46 mm/sec (3.97 km/day).

The shortest distances between the northern portions of the spawning grounds in the South Atlantic Bight to the collection site in the Marsh River and the Middle Atlantic Bight to the collection site in Sagadahoc Bay were estimated at 1350 km and 425 km respectively.

Statistical analysis

The relationship between fork length and the number of daily rings for juvenile bluefish captured in Maine during 1990–91 was described by linear regressions, where X is the $\log_{10}$ of fork length and Y is the number of daily rings. Slopes were then compared with ANCOVA. The curvilinear relationship of the same data from Maine (1990–91) and New York (1985–86) was described by quadratic equations, where X is fork length and Y is number of daily rings. The relationship of fork length to growth rate for combined data from Maine was described by a linear regression, where X is the fork length and Y is the rate of growth.

Results and discussion

Records of juvenile bluefish from the coast of Maine

Most records of juvenile bluefish were from southwestern Maine (York, Cumberland, Sagadahoc, and Lincoln counties) during the months of July, August, and September (Table 1). Fish varied in size from 37 to 197 mm FL (39–218 mm TL) from both oceanic and estuarine environments. Atlantic puffins (*Fratercula arctica arctica*), Arctic terns (*Sterna paradioaea*), and roseate terns (*Sterna dougallii dougalli*) were reported as feeding on young-of-year bluefish in July near Matinicus Rock and Seal Island (Knox County).[3] These observations indicated that juvenile bluefish occur in the offshore waters of Maine prior to their usual appearance inshore during August–September. Clark (1973) observed that juvenile bluefish remain where salinities are high when they first arrive, and later, as summer progresses, they penetrate into estuaries. Little Kennebec Bay (Table 1, No. 28) is the most northeast location where the capture of juvenile bluefish was confirmed. Three juvenile bluefish were among 1,000 age-1 Atlantic herring, *Clupea harengus*, tagged at this location on 25 August 1983 (Creaser and Libby, 1986).

Young-of-year (YOY) bluefish may be more abundant northeast of Boothbay Harbor than suggested by Table 1. The scarcity of information from this area

[3] Kress, S. Cornell Univ. Ornithology Lab, Ithaca, NY. Personal commun., January 1991.

Table 1

Unpublished records of juvenile bluefish, *Pomatomas saltatrix*, in Maine.

Location	N. Lat.	E. Long.	Date of capture	Oceanic (O) or estuarine (E)	No. captured	Size (mm)[1] TL	Size (mm)[1] FL	Method of capture[2]
Wells Harbor (York Co.)								
1 Wells Harbor	43°19'	70°34	Aug 1991	E	1	68		FN
Old Orchard Beach (York Co.)								
2 1 Mile off Amusement Pier	43°31'	70°21'	Summer 1961–1964	O	–	Juvenile		HL
Scarborough Marsh (Cumberland Co.)								
3 Confl. of Dunston, Libby, Nonesuch R.	43°33'	70°20'	Summer 1987	E		Juvenile		HL
Portland Harbor (Cumberland Co.)								
4 Union Wharf	43°39'15"	70°15'	Sept 1984	O	6	150–200		HL
5 SMVTI Dock	43°39'	70°14'15"	Sept 1986	O	–	130–150		HL
Royal River (Cumberland Co.)								
6 Royal River	43°47'30"	70°10'	Summer 1988	E	–	Juvenile		–
Merepoint (Cumberland Co.)								
7 Merepoint Bay	43°50'	70°00'01"	26 Sept 1991	E	97	150–174		GN
Jenny Island, Casco Bay (Cumberland Co.)								
8 Jenny Island	43°46'	69°55	16 July 1991	E	1	40		CT
New Meadows River (Cumb.–Sagadahoc Co.)								
9 Howard Pt., Thomas Bay	43°53'15"	69°53'10"	Aug 1988	E	3	70–130		FK
Kennebec River (Sagadahoc Co.)								
10 Atkins Bay	43°45'	69°48'	Summer 1981	E	–	80–90		HS
11 Winnegance Bay	43°53'	69°49'	Summer 1988–1990	E		50–150		HL
12 Bath Bridge	43°55'	69°48'30"	Summer 1982	E	90	<100		OT
13 Mouth of Androscoggin R.	43°57'	69°53'	5 Aug 1983	E	2	82–86		HS
14 Mouth of Abagadasset R.	44°00'30"	69°51'	17 July 1986	E	5	70–77		HS
Mouth of Abagadasset R.			11 Sept 1987	E	2	142–150		HS
Mouth of Abagadasset R			3 Aug 1989	E	8	52–76		HS
Mouth of Abagadasset R			3 July 1991	E	6	112–115		HS
Mouth of Abagadasset R			18 July 1991	E	2	84–94		HS
Sagadahoc Bay (Sagadahoc Co.)								
15 Kennebec Pt.	43°45'20"	69°45'45"	10–22 Aug 1990	O	29	39–70	37–64	HS
Montsweag Bay (Lincoln Co.)								
16 Berry Island	43°58'15"	69°40'55"	30 Aug 1972	E	1	112		HS
Berry Island			29 Aug 1973	E	2	132–141		HS
Berry Island			8 Sept 1974	E	4	125–140		HS
Sheepscot River (Lincoln Co.)								
17 Cross River	43°55'	69°37'	8 Aug 1991	E	1	115		HS
18 The Eddy	43°59'30"	69°39'	9 July 1991	E	3	80–85		HS
19 Marsh River	44°01	69°35'45"	14 Aug 1986	E	28	93–121		GN
Marsh River			26 Aug 1987	E	6	129–163		GN
Marsh River			8–28 Aug 1989	E	102	92–194		GN
Marsh River			1 Aug–26 Sept 1990	E	149	89–218	81–197	GN
Marsh River			17 July–17 Sept 1991	E	60	101–217	193–196	GN
20 Sheepscot Falls	44°02'45"	69°37'	Aug 1967	E		150–200		HL
21 Sheepscot River (town of Sheepscot)	44°03'30"	69°36'30"	2 Aug 1989	E	1	140		HL
Boothbay Harbor (Lincoln Co.)								
22 Lobster Cove	43°51'	69°37	30 Aug 1990	O	1	145	131	HL
Lobster Cove			11 Aug 1991	O	4	162–192		HL
23 Townsend Gut	43°50	69°39"	5 Sept 1985	O	1	Juvenile		HL
24 DMR Dock	43°50'45	69°38'30	14 Sept 1971	O	5	95–105	89–97	
DMR Dock			25 Aug 1978	O	1	86		DN
DMR Dock			4 July 1984	O	3	40–50		HL
25 Foot Bridge	43°51'	69°37'40	Summer 1970–1974	O		Juveniles, 2 sizes		HS
Matinicus (Knox Co.)								
26 Matinicus Rock	43°47	68°51'30	18 July 1986	O	1	77		AP
Matinicus Rock			5 July 1989	O	2	85–90		AP
Matinicus Rock			Mid July 1990	O	2	30–40		AT
Matinicus Rock			9–17 July 1991	O	14	40–50		AT

Table 1 (Continued)

Location	N. Lat.	E. Long.	Date of capture	Oceanic (O) or estuarine (E)	No. captured	Size (mm) TL	Size (mm) FL	Method of capture[2]
Matinicus Rock			24–30 July 1991	O	4	50–60		RT
Seal Island (Knox Co.)								
27 Seal Is.	43°53'	68°45'	July 1991	O	1	50		AT
Little Kennebec Bay (Washington Co.)								
28 Marston Pt.	44 39	67 26'15"	25 Aug 1983	O	3	100–130		HW

[1] TL = total length, FL = fork length

[2] OT = Otter trawl, FN = Fyke net, HL = Hook and line, -- = Unknown, HS = Haul seine, AP = Atlantic puffin, GN = Gill net, AT = Artic tern, DN = Dip net, CT = Common tern, HW = Herring weir, RT = Roseate tern

may result from the lack of scientific fish sampling activity and lack of familiarity with the identification of juvenile bluefish by the sportfishing public and finfish processors. Clark (1973) attributed high densities of juvenile bluefish in areas such as South Carolina and the New York Bight to sampling activity and availability of records from those areas.

Some published information exists on the distribution of juvenile bluefish in southwestern Maine. They have been reported from Casco Bay (Bigelow and Schroeder, 1953; Wilk, 1977), Boothbay Harbor (Lund, 1961) and Montsweag Bay (Targett and McCleave, 1974).

Length-frequency distributions

Length-frequency distributions of juvenile bluefish captured in the Marsh River (1990–91), Sagadahoc Bay (1990), and Merepoint Bay (1991) varied between 8 and 20 cm, 3 and 6 cm, and between 14 and 17 cm respectively (Fig. 2, A–D). Length-frequency data from the Marsh River was combined in 1-cm groupings and presented as one figure per year because fish were collected for only two months. Although the size range recorded during both 1990 and 1991 was similar, larger juveniles were more prevalent during 1991 (Fig. 2, A and B). The length-frequency composition of fish captured by beach seine from Sagadahoc Bay on 10 and 22 August 1990 (Fig. 2C) confirms the presence of small juveniles of 3–6 cm FL in Maine waters.

Previous reports of juvenile bluefish less than 70 mm from Wells Harbor, Winnegance Bay, the mouth of the Abagadasset River, Boothbay Harbor, Matinicus Rock and Seal Island have been presented in Table 1. The overall length-frequency range (8–20 cm FL) reported for fish captured in the Marsh River during 1 August–26 September 1990 and 17 July–17 September 1991 was similar to the length-frequency range reported from Great South Bay, New York (8–22 cm FL) during 28 May–12 August 1985 and 10 June–20 August 1986 (Nyman and Conover, 1988). Length-frequency distributions generated from gillnet catches (Fig. 2, A, B, D) are biased because panels of individual mesh sizes in gill nets are selective for specific sizes of fish.

Temperature and salinity data collected during gillnet sets

Juvenile bluefish were captured on both incoming (I) and outgoing (O) tides between 1 August and 26 September 1990 and between 17 July and 17 September 1991. Specific water temperatures do not appear to be associated with the arrival and departure of juvenile bluefish. Bluefish were first captured at water temperatures of 24.6–27.0°C (1990) and 22.8–24.0°C (1991). None were captured when the temperature dropped below 16.0°C (1990) and 19.3°C (1991). Water temperatures varied between 16.0 and 27.0°C (1990) and between 19.3 and 27.4°C (1991) when bluefish were present.

Lund and Maltezos (1970) reported that juveniles and adults appear at temperatures of 12–15°C and depart at temperatures of 13–15°C. Oben (1957) reported that juveniles appear at temperatures of 18–24.5°C and depart at 13–15°C. Similarly, Nyman and Conover (1988) reported that juveniles appear at 20–24°C and depart at water temperatures in the "middle-teens." We believe that juvenile bluefish arrived at the mouth of the Sheepscot River when the water temperature was relatively low and they were attracted to the Marsh River, 34.3 km upstream, by the warmer water. These fish appeared to remain in the Marsh River until the water temperature dropped to a temperature range that was lower than the water temperature at the time of their arrival in the sampling area.

The salinity of the Marsh River varied between 9.5 and 23.3 ppt (1990) and between 9.6 and 26.5 ppt (1991) when juvenile bluefish were present.

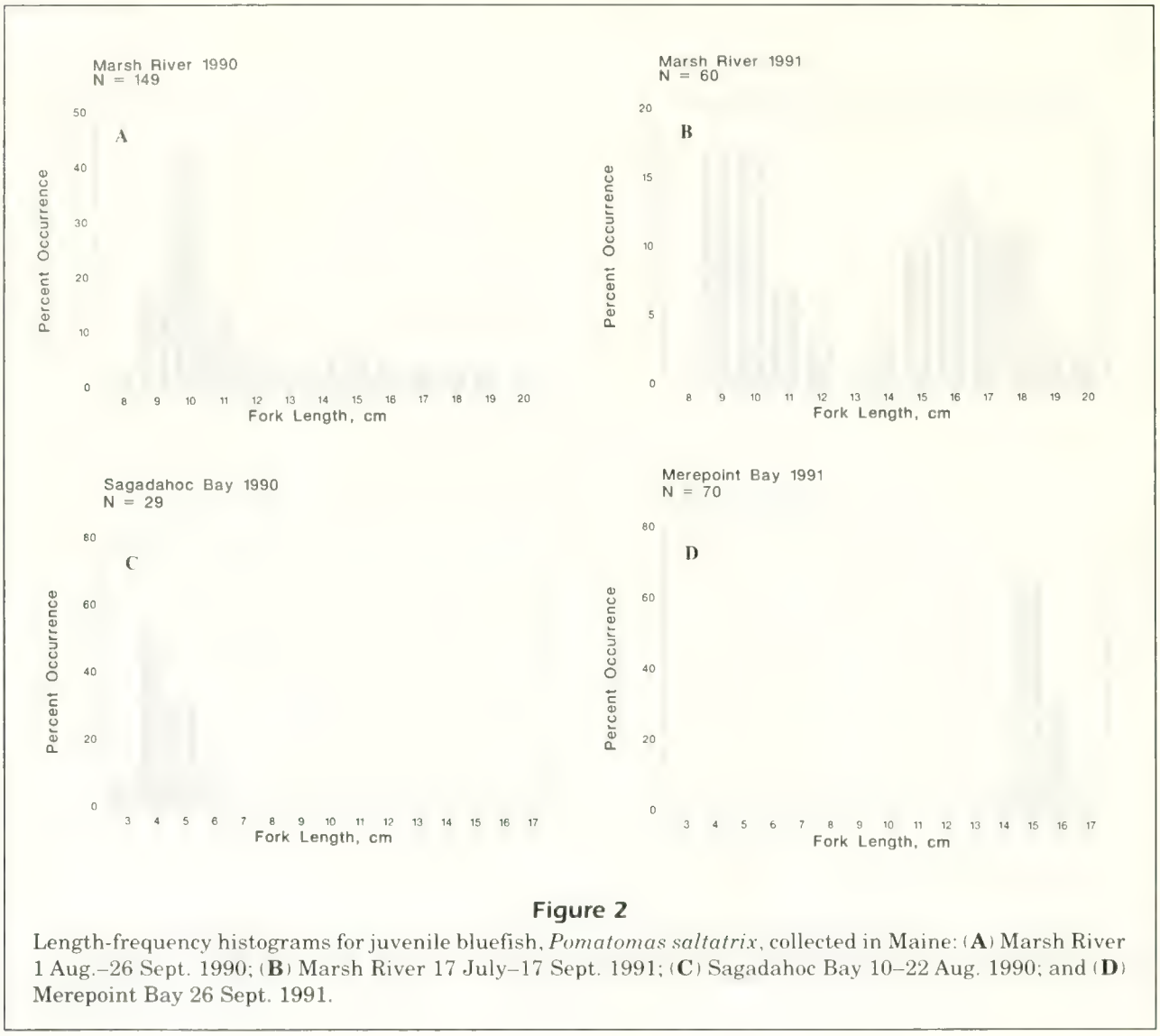

Figure 2

Length-frequency histograms for juvenile bluefish, *Pomatomas saltatrix*, collected in Maine: (**A**) Marsh River 1 Aug.–26 Sept. 1990; (**B**) Marsh River 17 July–17 Sept. 1991; (**C**) Sagadahoc Bay 10–22 Aug. 1990; and (**D**) Merepoint Bay 26 Sept. 1991.

Smale and Kok (1983) collected juveniles at 12–35 ppt, Clark (1973) occasionally found bluefish in very brackish water, and Baird (1873) captured juveniles from the freshwater portion of tidal rivers.

Stomach contents

Stomach contents of juvenile bluefish (81–200 mm FL) collected from the Marsh River in 1990 and 1991 are presented in Table 2. During 1990, fish were present in 81.4% of stomachs containing food (F), crustaceans in 39.5% (F), and plant material in 4.7% (F). During 1991, crustaceans were slightly more prevalent than fish. Crustaceans were present in 69.0% of stomachs containing food (F), fish in 62.1% (F), and plant material in 5.2% (F). The frequency of occurrence of polychaetes was 3.4% (F) and of insects, 1.7% (F).

During 1990 and 1991, crustaceans were the predominant prey items in terms of numbers of individuals observed (N) expressed as a percent of the total number of prey items recorded. Crustaceans composed 58.0% (1990) and 83.4% (1991) of the total prey items, fish composed 39.9% (1990) and 11.3% (1991), and plant material 2.0% (1990) and 4.5% (1991). During 1991, 0.5% and 0.3% of the total number of prey items were polychaetes and insects.

During 1990 and 1991, fish were the predominant prey in terms of wet or dry weight expressed as a percentage of the total wet weight (W) or dry weight (W1) of all prey species recorded. Fish composed 77.4% of total wet weight (W) and 79.9% of total dry weight (W1) during 1990 and 61.9% (W) and 67.5% (W1) during 1991. Crustaceans composed 22.5% (W) and 20.0% (W1) during 1990 and 37.3% (W) and

Table 2

The stomach contents of 149 juvenile bluefish, *Pomatomas saltatrix*, measuring 81–197 mm FL ($\bar{x}$ =117 mm), and 60 juveniles measuring 93–200 mm FL ($\bar{x}$ =142 mm), collected from the Marsh River, Maine, during 1 August–26 September 1990 and 17 July–17 September 1991, respectively.

	Marsh River 1990					Marsh River 1991				
Taxon	F (%)[1]	F1 (%)[2]	N (%)[3]	W (%)[4]	W1 (%)[5]	F (%)	F1 (%)	N (*) (%)	W (%)	W1 (%)
Class Crustacea										
Argulus sp.	1.550	1.342	1.024	0.021	0.027					
Corophium sp.						1.724	1.667	0.263 (0.606)	0.011	0.009
Crangon septemspinosa	34.884	30.201	55.631	22.351	19.888	63.793	61.667	26.579 (61.212)	37.294	31.830
Rhithropanopus harrisii	0.775	0.671	0.341	0.061	0.064					
Unidentified Crustacea	1.550	1.342	0.683	0.063	0.031					
Unidentified Isopoda	0.775	0.671	0.341	0.029	0.037					
Zoea of Majidae sp.						3.448	3.333	56.579	0.006	0.005
Total	39.535	34.228	58.020	22.525	20.046	68.966	66.667	83.421 (61.818)	37.310	31.844
Class Osteichthyes										
Alosa pseudoharengus	6.202	5.369	4.096	13.751	13.953					
Clupeidae spp.	5.426	4.698	2.730	7.392	8.045	15.517	15.000	3.158 (7.273)	27.131	29.792
Fundulus heteroclitus	0.775	0.671	0.683	7.309	9.239	1.724	1.667	0.526 (1.212)	6.720	7.366
Menidia menidia	9.302	3.054	5.119	13.229	13.798	8.621	8.333	1.579 (3.636)	2.471	2.228
Fish remains	59.690	51.678	27.304	37.739	34.861	36.207	35.000	6.053 (13.939)	25.589	28.146
Total	81.395	70.470	39.932	77.421	79.895	62.069	60.000	11.316 (26.061)	61.911	67.532
Class Polychaeta										
Polychaete remains					3.448	3.333	0.526	(1.212)	0.445	0.342
Total					3.448	3.333	0.526	(1.212)	0.445	0.342
Class Insecta										
Hymanoptera (unident.)					1.724	1.667	0.263	(0.606)	0.009	0.005
Total					1.724	1.667	0.263	(0.606)	0.009	0.005
Plant material										
Leafy	0.775	0.671	0.341	0.005	0.007					
Woody	3.986	3.356	1.706	0.049	0.052	5.172	5.000	4.474 (10.303)	0.325	0.278
Total	4.651	4.027	2.048	0.054	0.059	5.172	5.000	4.474 (10.303)	0.325	0.278

Number of stomachs examined	149	60
Number of stomachs containing food (% containing food)	129 (86.58)	58 (96.67)
Number of empty stomachs (% empty)	20 (13.42)	2 (3.33)
Mean wet weight/stomach (all stomachs) gm	0.651	1.133
Mean dry weight/stomach (all stomachs) gm	0.116	0.183
Mean wet weight/stomach (stomachs with food) gm	0.752	1.172
Mean dry weight/stomach (stomachs with food) gm	0.134	0.189

[1] F = % frequency of occurrence — the number of stomachs in which a species (taxon) occurred expressed as a % of the total number of stomachs containing food.
[2] F1 = % frequency of occurrence — the number of stomachs in which a species (taxon) occurred expressed as a % of the total number of stomachs examined.
[3] N = % numerical abundance — the number of individuals of each species (taxon) expressed as a % of the total number of food items (individual prey in stomachs) (*) designates the % numerical abundance excluding 215 zoea of Majidae found in the stomachs of two fish.
[4] W = % weight — wet weight of a species (taxon, prey category) expressed as a % of the total wet weight of food items.
[5] W1 = % weight — dry weight of a species (taxon, prey category) expressed as a % of the total dry weight of food items.

31.8% (W1) during 1991. Plant material accounted for 0.1% (W) and 0.1% (W1) during 1990 and 0.3% (W) and 0.3% (W1) during 1991. Polychaetes made up 0.4% (W) and 0.3% (W1) during 1991; insects made up 0.01% (W) and 0.01% (W1).

Stomach contents of juvenile bluefish collected from other areas in Maine during 1990 and 1991 are presented in Table 3. Bluefish measuring 150–173 mm FL were captured from Merepoint Bay on 9 September 1991. Fish were the predominant prey item

for all indices: 80.0% (F), 67.7% (N), 85.0% (W), and 88.6% (W1). Crustaceans composed 24.0% (F), 32.3% (N), 15.0% (W), and 11.4% (W1).

Bluefish measuring 37–64 mm FL were captured from Sagadahoc Bay on 10 and 22 August 1990. The predominant prey items recorded from these small juveniles were crustaceans (mysids and copepods). The frequency of occurrence of mysids and copepods in stomachs containing food (F) was 10.3% and 96.6%, respectively. Crustaceans were also the predominant prey items in terms of their wet or dry weight, expressed as a percentage of the total wet weight (W) or dry weight (W1). Crustaceans composed 82.2% of the total wet weight (W) and 80.0% of the total dry weight (W1). Fish remains were a minor constituent of the stomach contents of these small bluefish; they occurred in 6.9% of stomachs containing food (F). Fish also composed 17.7% of the total wet weight (W) and 21.0% of the total dry weight (W1). No information was available regarding the numbers of individuals observed (N) expressed as a percent of the total number of prey items recorded because copepod remains were so numerous that it was impractical to count them.

The diet of juvenile bluefish collected from the Marsh River in 1990 and 1991 and from Merepoint Bay in 1991 is consistent with observations by Breder (1922), Grant (1962), data for bluefish >10 cm reported by Smale and Kok (1983), and the 1981 results recorded in Friedland et al. (1988). All studies showed that the major portion of the diet (by weight or volume) of juvenile bluefish ≥8 cm in length consisted of fish. Although results presented by Lassiter (1962) and Naughton and Saloman (1984) are also consistent with this observation, Lassiter (1962) did not report bluefish lengths and some of the bluefish in Naughton and Saloman's (1984) data were older than age 1 (e.g. 39.9 cm).

Our findings regarding the diet of juvenile bluefish collected from Sagadahoc Bay (1990) were consistent with results presented by Kendall and Naplin (1981) and Smale and Kok (1983) for bluefish <100 mm. Smale and Kok (1983) reported that juvenile bluefish <100 mm feed predominantly on small crustaceans, and Kendall and Naplin (1981) stated that most of the diet of juvenile bluefish ($\bar{x}$=4.33 mm) consisted of copepods, copepodites, cladocera, and fish eggs. A transition to pisciverous feeding by juvenile bluefish at a size range between 60 and 100 mm has been reported (Nichols, 1913; Greeley, 1939; Oben, 1957; Clark, 1973; Smale and Kok, 1983). The transition to fish as prey had not yet occurred in bluefish measuring 37–64 mm from Sagadahoc Bay (Table 3).

On a per cent weight basis, the dominant prey species of juvenile bluefish (81–200 mm FL) collected from the Marsh River and Merepoint Bay included the mud shrimp *Crangon septemspinosa*, juvenile alewives, *Alosa pseudoharengus*, unidentified clupeids, Atlantic silversides, *Menidia menidia*, mum-

Table 3

The stomach contents of 34 juvenile bluefish, *Pomatomas saltatrix*, measuring 150–173 mm FL ($\bar{x}$=156 mm), collected from Merepoint Bay on 9 September 1991, and 29 small juveniles, measuring 37–64 mm FL ($\bar{x}$=48 mm), collected from Sagadahoc Bay, Maine, on 10 and 22 August 1990.

	Merepoint Bay 1991					Sagadahoc Bay 1990				
Taxon	F(%)	F1(%)	N(%)	W(%)	W1(%)	F(%)	F1(%)	N(%)	W(%)	W1(%)
Class Crustacea										
Crangon septemspinosa	24.000	17.647	32.258	14.973	11.400					
Mysidacea spp.						10.345	10.345	—	13.411	14.360
Copepod remains						96.552	96.552	—	68.746	64.621
Total	24.000	17.647	32.258	14.973	11.400	106.897	106.897		82.157	79.981
Class Osteichthyes										
Fish remains	68.000	50.000	58.065	40.057	42.353	6.897	6.897	—	17.742	21.019
Clupeidae spp.	12.000	8.824	9.677	44.970	46.247					
Total	80.000	58.824	67.742	85.027	88.600	6.897	6.897		17.742	21.019
Number of stomachs examined			34					29		
Number of stomachs containing food (% containing food			25 (73.53)					29 (100)		
Number of empty stomachs (% empty)			9 (26.47)					0 (0)		
Mean wet weight/stomach (all stomachs) gms			0.48288					0.03057		
Mean dry weight/stomach (all stomachs) gms			0.08890					0.00596		
Mean wet weight stomach (stomachs with food) gms			0.67367					0.03057		
Mean dry weight stomach (stomachs with food) gms			0.12091					0.00596		

michogs, *Fundulus heteroclitus*, and unidentified fish remains (Tables 2 and 3). Other authors reported that a significant portion of the juvenile bluefish diet consists of shrimp (Linton, 1905; Wilk, 1977; Friedland et al., 1988), clupeids (Hildebrand and Schroeder, 1928; Greeley, 1939; Grant, 1962; Richards, 1976; Naughton and Saloman, 1984), Atlantic silversides (Hildebrand and Schroeder, 1928; Greeley, 1939; Grant, 1962; Lassiter, 1962; Wilk, 1977; Friedland et al., 1988), and cyprinodontids (Greeley, 1939; Grant, 1962; Wilk, 1977). Prey of minor importance included *Argulus* sp., *Corophium* sp., *Rhithropanopus harrisii*, unidentified crustacea and isopods, zoea of Majidae sp., polychaete remains, unidentified *Hymenoptera*, and both leafy and woody plant material (Table 2). Estuaries in Maine are probably seasonal nursery grounds where high prey densities and warm water temperatures result in rapid growth.

During 1990 and 1991, 13.42% and 3.33% of the fish collected in the Marsh River and 26.47% (1991) of the fish collected in Merepoint Bay possessed empty stomachs (Tables 2 and 3). With the exception of the 16% estimate reported by Grant (1962), who also used gill nets, the percent of empty stomachs reported by several investigators varied between 30 and 87%. Perhaps the low incidence of empty stomachs reported in our studies resulted from the use of gill nets, which constrict the gills and esophagus thus reducing the possibility of regurgitation.

An analysis of daily growth increments on otoliths

Growth increments on the otoliths of many species of juvenile fishes, including bluefish, are produced on a daily basis as long as growing conditions are adequate (Nyman and Conover, 1988). Bluefish collected from the Marsh River displayed 94–200 ($\bar{x}$=126) and 97–176 ($\bar{x}$=134) daily growth increments during 1990 and 1991, respectively. Fish collected from Sagadahoc Bay (1990) displayed 58–93 ($\bar{x}$=66) daily growth increments, and fish collected from Merepoint Bay (1991) displayed 125–146 ($\bar{x}$=134) daily growth increments. First ring deposition occurs approximately 2–4 days after spawning (Nyman and Conover, 1988) so these daily growth increments correspond to a total of approximately 129 days (Marsh River, 1990), 137 days (Marsh River, 1991), 69 days (Sagadahoc Bay, 1990), and 137 days (Merepoint Bay, 1991) of growth after spawning.

Spawning occurs somewhere along the Atlantic coast during practically every month of the year (Table 4). Several "seasonal" periods of significant spawning are evident. Major spawning periods occur during the "spring" (March–May) in the South Atlantic Bight and "summer" (May–September) in the Middle Atlantic Bight. A minor "fall-winter" (Kendall and Walford, 1979) and perhaps "summer-fall" (Collins and Stender, 1987) spawning period also occurs in the South Atlantic Bight.

It is unlikely that juvenile bluefish captured in the Marsh River during the spring and in Sagadahoc Bay during the summer originated from the major spring spawning in the South Atlantic Bight or the major summer spawning in the Middle Atlantic Bight. Most juvenile bluefish from the Marsh River originated from a spring spawning during March–May (Fig. 3, A and B). Conservative estimates of the time required to swim from the northern portion of the spawning ground in the South Atlantic Bight to the collection site in the Marsh River during 1990 and 1991 would equal 147 days (1350 km ÷ 9.16 km/day) and 156 days (1350 km ÷ 8.64 km/day), respectively. These estimates of swimming time exceed the known ages of juvenile bluefish derived from daily ring counts (129 days, 1990; 137 days, 1991) even before additional time from physical and biological factors are considered. These factors include 1) swimming into the current from Cape Hatteras to Southwestern Maine (Bumpus and Lauzier, 1965), 2) the possibility that swimming speed is less than twice the body length, 3) decreased swimming speed at night (Olla et al., 1985), and 4) feeding behavior which results in nonlinear movement.

Juvenile bluefish from Sagadahoc Bay originated from a summer spawning which occurred mainly during June (Fig. 3C). A conservative estimate of the time required to swim from the northern portion of the spawning ground in the Middle Atlantic Bight to the collection site in Sagadahoc Bay during 1990 would equal 107 days (425 km ÷ 3.97 km/day). This estimate greatly exceeds the known age of the fish (69 days). The estimate of swimming time is increased further when physical and biological factors that impede swimming are considered.

We believe that juvenile bluefish collected from the Marsh River and Sagadahoc Bay may be derived from unknown spawning areas closer to Maine. Lyman (1974) stated that "some of their spawning grounds are known but many remain to be discovered along much of the northeast coast." It is also possible that both major spawning areas known to exist in the South and Middle Atlantic Bights, have extended northward. Another possibility is that "larval transport mechanisms and spawning periodicities for bluefish are considerably more complex than previously believed" (Powles, 1981).

The relationship between the $\log_{10}$ of the fork length and the number of daily rings for 1990 and 1991 data is shown in Figure 4. The range of fish

Table 4

Seasonal spawning dates of bluefish, *Pomatomas saltatrix*, in the South and Middle Atlantic Bight.

Author	Location	Months of spawning												Evidence of spawning	Size
		M	A	M	J	J	A	S	O	N	D	J	F		
South Atlantic Bight															
[illegible] and Stetter 1987	Cape Canaveral, FL–Cape Fear, NC													larvae present	≤4 mm SL
	Coast of Georgia and Florida													larvae present	<4 mm SL
[illegible] et al. 1979	Outer shelf S. Atlantic Bight													larvae present	≤10 mm SL
	Offshore South of Cape Hatteras, NC													fall and winter spawning	
Nyman and Conover 1988	Long Island, NY													spawning date backcalculated	—
[illegible] 1887	Lake Worth and Jupiter Inlet, FL													ripe adults	—
Powles 1981	Cape Canaveral, FL–Cape Fear, NC													larvae present	no size given
Middle Atlantic Bight															
Baird 1874	Fort Macon, NJ													ripe and running adults	—
Chiarella and Conover 1990	Off New York													analysis of gonads	—
DeSylva et al. 1962	Indian River Inlet, DE													larvae present	4 mm SL
Deuel et al. 1966	Jones east of Fire Island Inlet, Long Is., NY													ripe and running female	—
Herman 1963	Narragansett Bay, RI													larvae present	3.12 mm SL
Kendall and Naplin 1981	Ocean City, MD													larvae present	4.33 mm SL
Kendall and Walford 1979	Midway over continental shelf of Mid-Atlantic Bight													larvae present	<10 mm SL
Morse et al. 1987	Cape Hatteras, NC, to Long Is., NY													larvae present	no size given
Norcross et al. 1974	Outer shelf off Virginia–N. Carolina													eggs present	—
	Outer shelf off Virginia–N. Carolina													larvae present	2.0–16.5 mm SL
Nyman and Conover 1988	Hudson River, NY													spawning date backcalculated	—
Pearson 1941	Mouth of Chesapeake Bay, VA													larvae present	4–7 mm SL
Perlmutter 1939	Southern Long Island Shore, NY													ripe and running female	—
Sherman et al. 1984	NE United States													larvae present	3.5–28 mm SL

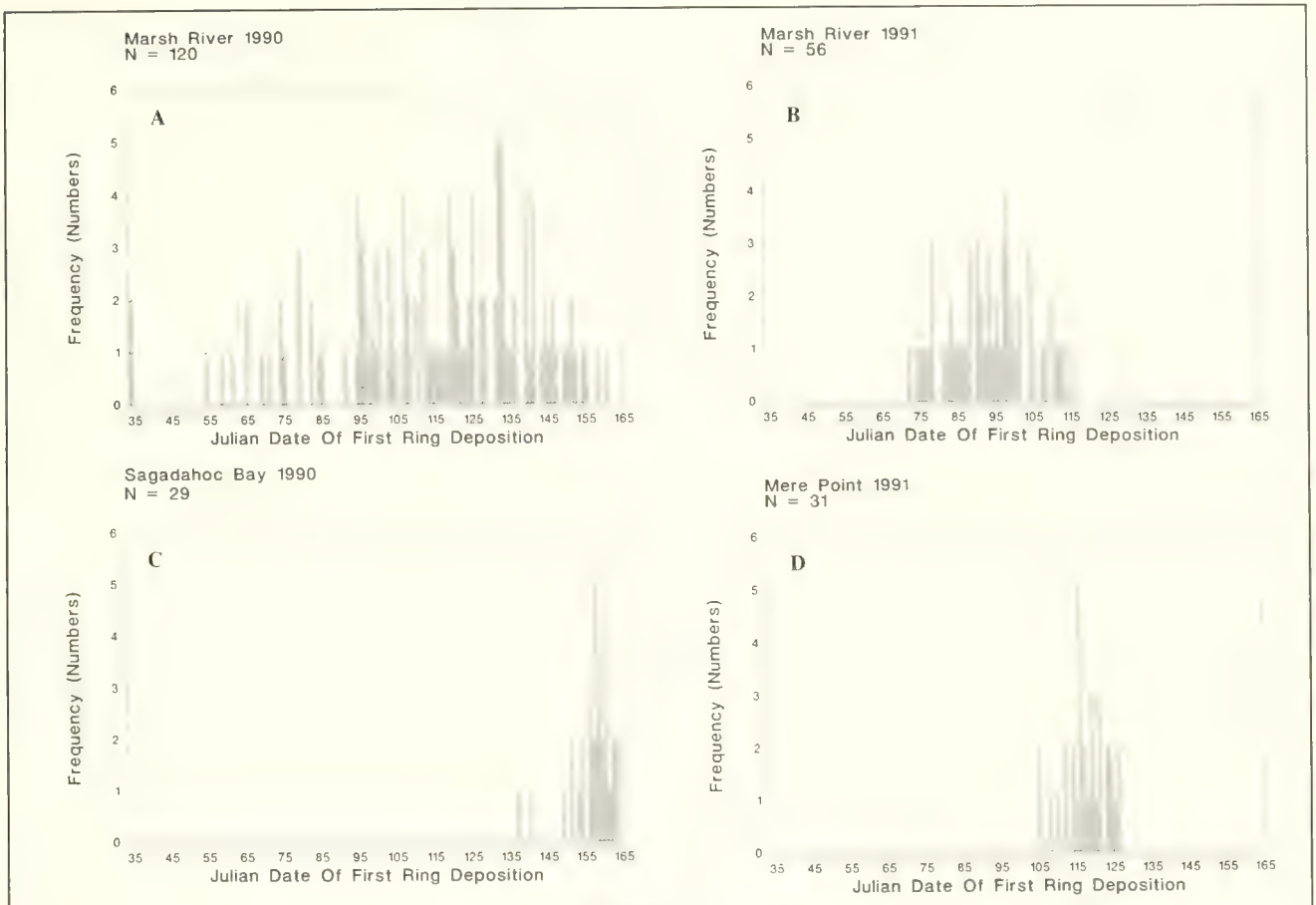

Figure 3

Estimated dates of ring deposition in otoliths of juvenile bluefish, *Pomatomas saltatrix*, collected in Maine: (**A**) Marsh River 1990; (**B**) Marsh River 1991; (**C**) Sagadahoc Bay 1990; and (**D**) Merepoint Bay 1991.

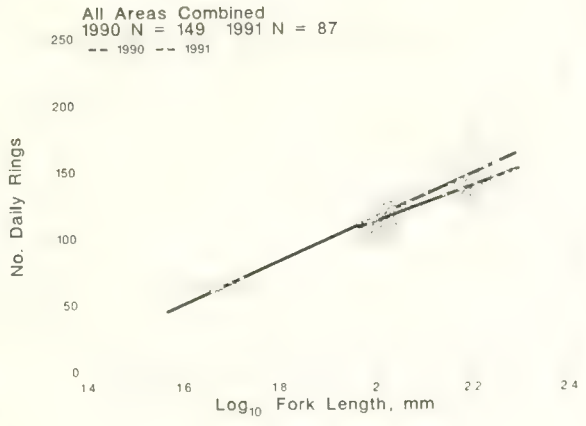

Figure 4

The relationship between $\log_{10}$ fork length (X) and the number of daily rings (Y) for juvenile bluefish, *Pomatomas saltatrix*, captured in Maine during 1990–91. The regression equations are $Y = -209.891 + 162.6751 \log_{10} X$, R^2=0.834, for 1990 and $Y = -151.461 + 132.0466 \log_{10} X$, $R^2 = 0.629$, for 1991.

lengths recorded during 1991 (93–200 mm) was small compared with 1990 (37–197 mm). The number of daily growth rings varied between 58 and 200 (1990) and between 97 and 176 (1991). Although an ANCOVA revealed that the slopes of the relationship of $\log_{10}$ fork length to number of daily rings differed significantly between years (P<0.05), the significance of this is questionable because the size range of fish also differed between years. Nyman and Conover (1988) analyzed similar regressions for juvenile bluefish captured in New York waters during 1985 and 1986 and found significant differences in slopes between years. Individual values for fork lengths and daily ring counts collected in New York waters during 1985–1986 obtained from Robert Nyman[4] were fit to quadratic equations and compared to similar values obtained in Maine during 1990–91 (Fig. 5). Fork lengths varied between 41 and 166 mm (1985) and between 31 and 167 mm (1986).

[4] Nyman, R. U.S. Environmental Protection Agency, 401 M St., SW, Washington, DC 20460. Personal commun., June 1991.

The number of daily growth rings varied between 44.3 and 160.0 (1985) and between 42.7 and 133.0 (1986). Fish captured in New York grew faster. This may have resulted from shorter migrations, longer exposure to warm water, or better food or feeding conditions. Raw data plots from which New York information (Fig. 5) were derived are presented in Nyman and Conover (1988, fig. 9).

The growth rate increased from about 0.7 mm/day to about 1.25 mm/day as fish length increased from 50 mm to 200 mm FL (Fig. 6). The mean growth rate was 0.96 mm/day. Nyman and Conover (1988) reported a growth rate of approximately 1.3 mm/day for fish obtained from field collections over a 61-day period.

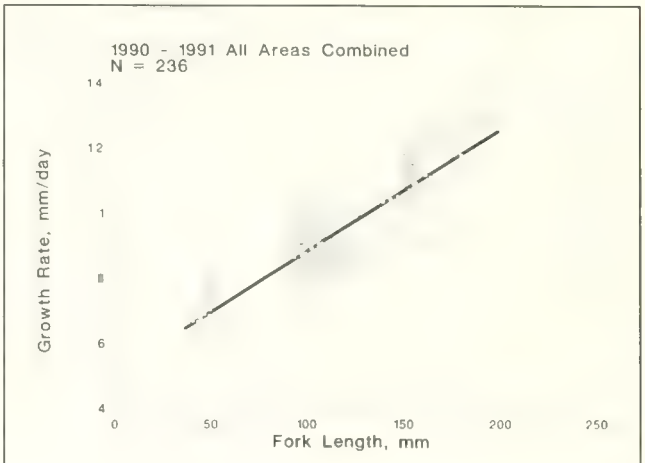

Figure 6

The relationship of fork length to growth rate for juvenile bluefish, *Pomatomas saltatrix*, collected in Maine during 1990–1991. The regression equation is $Y = 0.50990 + 0.00372X$, $R^2 = 0.750$.

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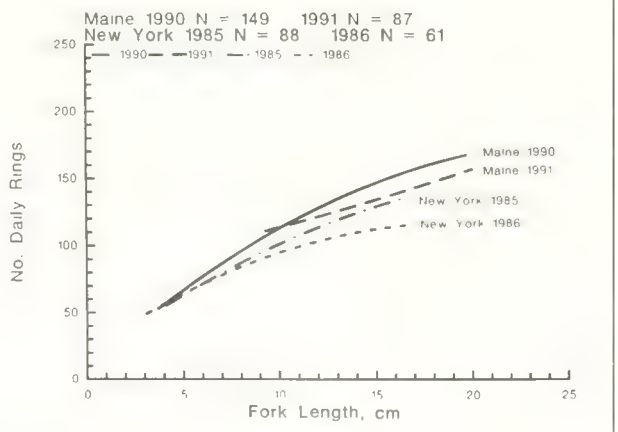

Figure 5

A comparison of the relationship of fork length to number of daily rings for juvenile bluefish, *Pomatomas saltatrix*, from Maine and New York. The regression equations are $Y = 8.53468 + 12.89328X - 0.24416X^2$, $R^2 = 0.847$, for Maine 1990; $Y = 79.49049 + 2.97353X + 0.4563X^2$, $R^2 = 0.635$, for Maine 1991; $Y = 15.19726 + 10.63463X - 0.20203X^2$, $R^2 = 0.840$, for New York 1985; and $Y = 20.22134 + 10.12947X - 0.26495X^2$, $R^2 = 0.835$, for New York 1986.

Literature cited

Baird, S. F.
1873. Condition of the sea fisheries of the south coast of New England in 1871–1872. U.S. Comm. Fish Fisheries. Parts 1 and 2: The bluefish, p. 235–252.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. Fish. Bull. 53:1–577.

Breder, C. M., Jr.
1922. Observations on young bluefish. Copeia 106:33–36.
Briggs, J. C.
1960. Fishes of world-wide (circumtropical) distribution. Copeia 3:171–180.
Bumpus, D. F., and L. M. Lauzier.
1965. Serial atlas of the marine environment. Folio 7: Surface circulation on the continental shelf off eastern North America between Newfoundland and Florida. Am. Geographical Soc., New York, NY, 23 p.
Chiarella, L. A., and D. O. Conover.
1990. Spawning season and first-year growth of adult bluefish from the New York Bight. Trans. Am. Fish. Soc. 119:455–462.
Clark, J. R.
1973. Bluefish. *In* A. L. Pacheco (ed.), Proceedings of a workshop on egg, larval, and juvenile stages of fish in Atlantic coast estuaries. National Marine Fisheries Service, Middle Atlantic Coast Fisheries Center, Technical Publication 1, Highlands, NJ, p. 250–251.
Collins, M. R., and B. W. Stender.
1987. Larval king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*S. maculatus*), and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States 1973–1980. Bull. Mar. Sci. 41:822–834.
Creaser, E. P., and D. A. Libby.
1986. Tagging of age 1 herring (*Clupea harengus* L.) and their movement along the Maine and New Brunswick Coasts. J. Northwest Atl. Fish. Sci. 7:43–46.
Deuel, D. G., J. R. Clark, and A. J. Mansueti.
1966. Description of embryonic and early larval stages of bluefish, *Pomatomus saltatrix*. Trans. Am. Fish. Soc. 95:264–271.
Friedland, K. D., G. C. Garman, A. J. Bejda, A. L. Studholme, and B. Olla.
1988. Interannual variation in diet and condition in juvenile bluefish during estuarine residency. Trans. Am. Fish. Soc. 117:474–479.
Grant, C. C.
1962. Predation of bluefish on young Atlantic menhaden in Indian River, Delaware. Chesapeake Sci. 3:45–47.
Greeley, J. C.
1939. Fishes and habitat conditions of the shore zone based upon July and August seining investigations. *In* A biological survey of the salt waters of Long Island. 1938. Part II. Suppl. to 28th Ann. Rep. No. XV, New York Cons. Dep., Albany, NY, p. 72–91.
Harden Jones, F.
1968. Fish migration. St. Martin's Press, New York, NY, 325 p.
Herman, S. S.
1963. Planktonic fish eggs and larvae of Narragansett Bay. Limnol. Oceanogr. 8:103–109.
Hildebrand, S. F., and W. C. Schroeder.
1928. Fishes of Chesapeake Bay. Bull. Bur. Fisheries 43:231–234.
Hubbs, C. L., and K. F. Lagler.
1958. Fishes of the Great Lakes region. Cranfield Inst. Sci., Bloomfield Hills, MI, 213 p.
Hynes, H. B. N.
1950. The food of fresh water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J. Animal Ecol. 19:36–58.
Kendall, A. W., and N. A. Naplin.
1981. Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight. Fish. Bull. 79:705–726.
Kendall, A. W., and L. A. Walford.
1979. Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fish. Bull. 77:213–227.
Lassiter, L. L.
1962. Life history aspects of the bluefish, *Pomatomus saltatrix* (Linnaeus) from the coast of North Carolina. M.S. thesis. North Carolina State College, Raleigh, NC, 103 p.
Linton, E. D.
1905. Parasites of fishes of Beaufort, North Carolina. Bull. U.S. Bur. Fish. (1904) 24:321–348.
Lund, W. A.
1961. A racial investigation of the bluefish, *Pomatomus saltatrix* (Linnaeus), of the Atlantic coast of North America. Boletin del Instituto Oceanografico Venezuela 1 (1):73–129.
Lund, W. A., and G. C. Maltezos.
1970. Movements and migrations of the bluefish, *Pomatomus saltatrix*, tagged in waters of New York and southern New England. Trans. Am. Fish. Soc. 99:719–725.
Lyman, H.
1974. Successful bluefishing. Int. Marine Publ. Company, Camden, ME, 22 p.
Morse, W. W., M. P. Fahat, and W. G. Smith.
1987. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1977–1984), Atlas No. 2. Annual distribution patterns of fish larvae. U.S. Dep. Commer., NOAA Tech. Memo NMFS-F/NEC-47, 215 p.
Naughton, S. P., and C. H. Saloman.
1984. Food of bluefish (*Pomatomus saltatrix*) from the U.S. South Atlantic and Gulf of Mexico. NOAA Tech. Memo NMFS-SEFC-150, 37 p.
Nichols, J. T.
1913. Concerning young bluefish. Trans. Am. Fish. Soc. 43:169–172.
Norcross, J. J., S. L. Richardson, W. H. Massmann, and E. B. Joseph.
1974. Development of young bluefish (*Pomatomus saltatrix*) and distribution of eggs and young in Virginia coastal waters. Trans. Am. Fish. Soc. 103:477–497.

Nyman, R. M., and D. O. Conover.
1988. The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. Fish. Bull. 86:237–250.

Oben, L. C.
1957. About the drifting approach of fingerline bluefish (*Pomatomus saltatrix* (Linnaeus)) to the shores of the Black Sea in the Karadaga region (1947–1954). Karadagskaia Biol. Stn. Tr. (4):155–157.

Olla, B. L., A. L. Studholme, and A. J. Bejda.
1985. Behavior of juvenile bluefish, *Pomatomus saltatrix*, in vertical thermal gradients: influence of season, temperature, acclimation and food. Mar. Ecol. Prog. Series 23:165–177.

Pearson, J. C.
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout, *Cynoscion regalis* (Bloch). U.S. Fish. Wildl. Serv., Fish. Bull. 50:79–102.

Perlmutter, A.
1939. An ecological survey of young fish and eggs identified from tow-net collections. Section I. *In* A biological survey of the salt waters of Long Island. 1938. Part I. Suppl. to 28th Ann. Rep. No. XV, New York Conserv. Dep., Albany, NY, p. 11–71.

Pierce, H. D.
1883. The spawning of bluefish and opinion of the cause of mortality of fish in the Gulf of Mexico. Bull. U.S. Fish. Comm. 1882–1883, p. 332–333.

Powles, H.
1981. Distribution and movements of neustonic young of estuarine dependent (*Mugil* spp., *Pomatomus saltatrix*) and estuarine independent (*Coryphaena* spp.) fishes off the southeastern United States. Rapp. P.-v. Reun. Cons. int. Explor. Mer 178:207–209.

Richards, S. W.
1976. Age, growth, and food of bluefish (*Pomatomus saltatrix*) from east-central Long Island Sound from July through November 1975. Trans. Am. Fish. Soc. 105:523–525.

Scott, W. B., and M. G. Scott.
1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219, 731 p.

Sherman, K., W. Smith, W. Morse, M. Berman, J. Greed, and L. Ejsymont.
1984. Spawning strategies of fishes in relation to circulation,phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser. 18:1–19.

Smale, M. J., and H. M. Kok.
1983. The occurrence and feeding of *Pomatomus saltatrix* (elf) and *Lichia amia* (leervis) juveniles in two Cape south coast estuaries. S. Afr. J. Zool. 18:337–342.

deSylva, D. P., F. A. Kalber Jr., and C. N. Shuster Jr.
1962. Fishers and ecological conditions in the shore zone of the Delaware River estuary, with notes on other species collected in deeper waters. Univ. Del. Mar. Lab. Inf. Ser. Publ. 5, 164 p.

Targett, T. E., and J. D. McCleave.
1974. Summer abundance of fishes in a Maine tidal cove with special reference to temperature. Trans. Am. Fish. Soc. 103:325–330.

U.S. Department of Commerce.
1990–1991. Tide tables of the east coast of North and South America. U.S. Dep. Commer., NOAA, Natl. Ocean Surv., Rockville, MD.

Wilk, S. J.
1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). Sandy Hook, NMFS Tech. Ser. Rep. No. 11, 56 p.

Windell, J. T.
1971. Food analysis and rate digestion. IBP (International Biological Programme) Handbook 3:215–226.

Abstract.—Most red drum, *Sciaenops ocellatus*, age and growth research has utilized sagittal otoliths. We evaluated the other otoliths, the lapilli and asterisci, as well as the sagittae, as ageing structures and length-at-age estimators in hatchery-reared and wild juveniles (<50 mm SL). Our otolith mounting and sectioning protocol for preparing sagittal sections required significantly less processing time with no loss in accuracy than the more traditional transverse sectioning reported in the literature. Increments in asterisci were clearly visible from the primordium to the otolith margin, whereas the nuclear region of sagittae and lapilli were more opaque and prevented detection of all rings. Asterisci were not present at hatching, but on average form six days later, therefore the addition of a constant (6 days) to the ring counts of asterisci resulted in this otolith providing more accurate ages than sagittae or lapilli. According to coefficients of determination (r^2) generated from the relation between fish length and otolith diameter, the sagitta, asteriscus, and lapillus predict fish length in descending order. However, because inner rings on sagittae were usually undetectable, lengths at ages cannot accurately be predicted. All rings are observable in the asteriscus; thus, by using the 6-day adjustment factor accurate length-at-age prediction is possible.

Differences between the sagitta, lapillus, and asteriscus in estimating age and growth in juvenile red drum, *Sciaenops ocellatus*

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The red drum, *Sciaenops ocellatus*, is a recreationally and commercially important marine fish ranging throughout the Gulf of Mexico and along the Atlantic seaboard to Massachusetts. An estuarine-dependent species, red drum spawn offshore, and juveniles move to estuarine nursery areas. After reaching sexual maturity at about age 5 (Mercer, 1984), these fish migrate offshore, where they aggregate into large schools. Concern for the declining status of the resource has prompted many Gulf of Mexico and Atlantic states to implement research to provide a sound scientific basis for management. This research includes aspects of early life history important to recruitment processes (Holt et al., 1983), age and growth (Peters and McMichael, 1987; Comyns et al., 1989), artificial propagation (Arnold, 1988), behavior (Fuiman and Ottey, 1993), and spawning stock abundance (Comyns et al., 1991).

An overwhelming percentage of age and growth investigations have utilized the sagittae because they are the largest of the three otoliths and therefore the easiest to extract and examine (Irie, 1960; Campana and Neilson, 1985). Since Panella (1971) first identified daily growth increments in sagittal otoliths, the formation of daily rings has been confirmed in many species (Jones, 1986).

References to the lapillus are uncommon in the literature. Bailey and Stehr (1988) reported use of the lapillus to age larval walleye pollock, *Theragra chalcogramma* (Pallas), younger than 20 days because it was larger than the sagitta up to that age. Brothers and McFarland (1981) used lapilli to age juvenile French grunts, *Haemulon flavolineatum*. References to the use of the asteriscus in ageing are unknown.

Previous ages for red drum larvae (Comyns et al., 1989) and juveniles (Peters and McMichael, 1987) were derived from sagittae. Peters and McMichael (1987) found that the inner ring structure was usually unclear in juveniles. They used ten larval otoliths to measure the distance from the primordium to the tenth ring, then began juvenile ring counts with the eleventh ring, 56 µm

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from the primordium (the mean distance to the tenth ring from the ten larval otoliths). The juvenile otoliths were transversely sectioned and glycerin-cleared. This method was verified by examination of the innermost rings from exceptionally clear juvenile otoliths.

We examined sagittae, lapilli, and asterisci to determine the best ageing structure for juvenile red drum by comparing ring counts for each otolith with known ages in hatchery-reared fish. We also evaluated the relation between fish length and otolith diameter for use in backcalculating lengths at age from each otolith. We report the size at which otoliths are formed to evaluate possible biases in age estimations.

Materials and methods

Wild-caught and known-age (laboratory-reared) juvenile red drum were preserved in 70% ethanol. Standard lengths of fish were measured to the nearest 0.1 mm prior to the removal of otoliths. We made no attempt to measure shrinkage due to preservation or to adjust our measurements accordingly. Otoliths were extracted between crossed polaroids by using a dissecting microscope at 6–12× magnification and transmitted light. This procedure exploited the birefringence of the crystalline structure of otoliths and greatly aided otolith location and removal. Extraneous tissue was removed, and the otoliths were mounted concave side up on glass slides. Two mounting media were used, thermoplastic cement and a polymer mounting medium. The thermoplastic cement allowed easier otolith manipulation and the polymer provided a less brittle and more transparent mount. Otoliths were ground in the sagittal plane with 600-grit carborundum paper and polished with 0.9-μm aluminum oxide sheets prior to examination under a compound microscope. Otoliths mounted with thermoplastic cement were ground to the primordium, flipped convex side up, and again ground to the primordium. Polymer mounted otoliths were ground to the primordium from the concave side. The polished otoliths were illuminated with plane-polarized transmitted light to optimize ring resolution. Ring counts were determined at 125–250× for sagittae and at 250–500× for lapilli and asterisci. To avoid bias from sequentially ageing all three otoliths from the same fish, all sagittae were aged first, followed by all lapilli and all asterisci. After ageing, mean ring counts, standard deviations, and coefficients of variation were calculated.

Otolith diameters (μm) were measured with a digital image analysis system (Optimas ver 3.01, Bioscan, Edmunds, WA). Otolith diameter was defined as a chord from the anterior rostrum to the posterior edge, passing through the primordium. The relationship between standard length and otolith diameter was examined by plotting otolith diameter on standard length and calculating the regression.

We examined larvae and juveniles to determine the size at which otoliths were formed. Larvae were translucent under transmitted polarized light, so otoliths were observable without dissection in fish as small as 4.0 mm SL. To precisely determine fish size at asteriscus formation, five larvae between 2.7 and 3.5 mm SL were dissected and the disrupted otic capsules mounted on glass slides with polymer mounting medium and examined microscopically.

Results

Wild-caught fish ranged from 15 to 50 mm SL, and laboratory-reared fish ranged from 18 to 25 mm SL. Fifty laboratory-reared and 70 wild-caught juveniles were processed; six otoliths were removed from each fish. The sagittae were used as landmarks to locate the smaller lapilli and asterisci. The lapilli were anterior and distal to the sagittae, and the asterisci were posterior and proximal to the sagittae. The asterisci were often found attached to the saccular tissue removed with the sagittae. To determine the size at otolith formation, we examined 35 wild-caught red drum larvae ranging from 1.3 to 7.0 mm SL. Sagittae and lapilli were present in all larvae examined. Asterisci were found in all dissected fish ≥3.0 mm SL (n=5) and not detected in fish smaller than 2.8 mm SL (n=3). In specimens that were not dissected, asterisci were first observed in larvae 3.8 mm SL and were present in all larvae larger than 4.0 mm SL.

Considerable differences were found in the general size and shape of the otoliths (Fig. 1). All otoliths were spherical or slightly ovoid in larvae ≤5 mm SL. Sagittae in larvae ≥5 mm SL began to develop a rostral process, and sagittae of 10-mm larvae were oval, laterally compressed, and had developed a prominent rostrum. The general shape of sagittae did not change in fish 10–50 mm SL. Lapilli followed the same initial development, but the posterior margin of these otoliths became scalloped when larvae were approximately 15 mm SL owing to the formation of numerous accessory primordia. Initially asterisci were also spherical, but the axis of growth changed, with subsequent development resulting in a kidney-shaped appearance by 15 mm SL. Accessory primordia were seldom observed in sagittae and were not observed in asterisci. Lapilli and asterisci were similar in size; however, the diameter of sagittae was approximately three times larger and grew approximately five times faster than asterisci and lapilli (Fig. 2).

Diameters of asterisci and lapilli were well correlated with standard length, but the strongest relation between otolith diameter and standard length was observed in sagittae (Fig. 2). Anterior rostra and

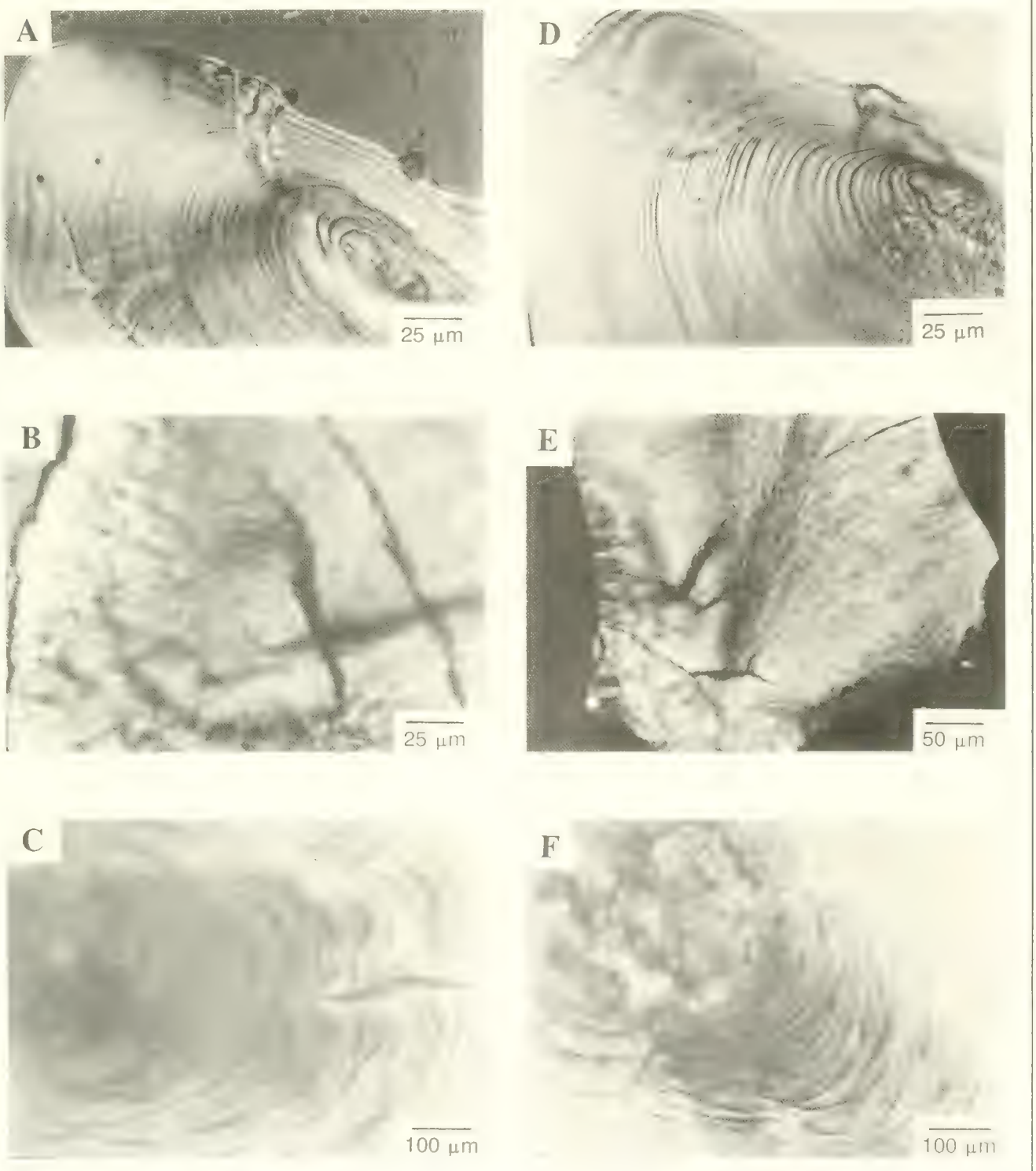

Figure 1

Red drum, *Sciaenops ocellatus*, otoliths: (**A**) hatchery asteriscus 500×; (**B**) hatchery lapillus 500×; (**C**) hatchery sagitta 125×; (**D**) wild asteriscus 500×; (**E**) wild lapillus 250×; (**F**) wild sagitta 125×.

otolith primordia were well defined in sagittae, which, along with a uniform axis of growth, resulted in a more consistent axis of measurement. The lapillus and asteriscus were more circular in shape than the sagitta and had a less well-defined anterior rostrum. The lapillus also formed accessory primordia, which were reflected in an irregular perimeter. Although accessory primordia were not observed in asterisci, the axis of growth shifted with development, resulting in diameter measurements through the primordia that did not necessarily reflect the maximum otolith diameter. These features resulted in greater variability of diameter measurements for asterisci and lapilli than for sagittae.

The accuracy and precision of age estimates varied among otoliths. Fish used to estimate daily ages were collected 46 days after hatching. Although increments were present in all three otoliths, the definition and resolution of the rings differed, especially near the primordia. The mean ring counts, standard deviations, and coefficients of variation are presented in Table 1. All increment widths exceeded the limit of resolution for light microscopy by more than an order of magnitude (Jones and Brothers, 1987; David and Paul, 1989). All ring counts substantially underestimated the age of the 46-day-old hatchery-reared fish. The asteriscus underestimated the true age by 6 days, while sagittae and lapilli underestimated age by 21 days and 25 days, respectively. To obtain realistic age estimates using asterisci, ring counts were adjusted because that otolith is not formed at hatching, but age estimates from ring counts in lapilli and sagittae were erroneously low because all rings could not be observed and counted because of poor contrast in the nuclear region. In addition to providing the most accurate age, coefficients of variation indicated that the asteriscus was also the most precise indicator of true age.

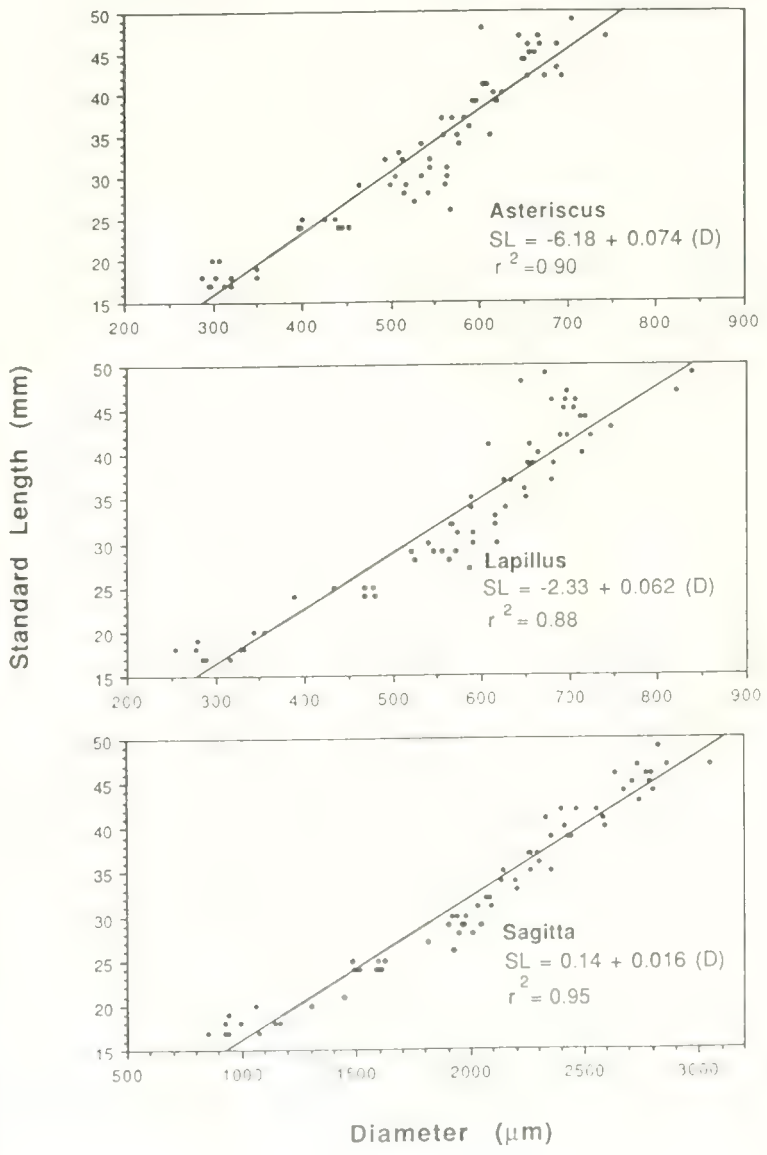

Figure 2

Fish length and otolith diameter relationships for each otolith type of red drum, *Sciaenops ocellatus*. Otolith diameter (μm) plotted on standard length (mm) with linear regression lines overlaid (n=70).

Discussion

Shrinkage of larvae due to preservation has been found to be significant (Blaxter, 1971; Theilacker and Dorsey, 1980; Hay, 1982; Brothers et al., 1983; and Leak, 1986). We did not adjust length measurements for shrinkage due to preservation because most specimens were juveniles (15–50 mm SL), and because we immediately fixed specimens in ethanol which has been shown to minimize the problem of shrinkage (Radke, 1989).

Daily increment formation has been validated in sagittae by using laboratory-reared red drum that were up to 21 days posthatch (Peters and McMichael, 1987). The 6-day underestimate in age determined from the asteriscus of known-age (hatchery-reared) fish corresponded well with age at otolith formation (6–7 days)

Table 1

Comparison of ages derived from sagittal sections of each otolith type in known age (46 days), hatchery-reared red drum, *Sciaenops ocellatus*. Values are reported for mean age, standard deviation, and coefficient of variation.

Otolith	*N*	Mean age (d)	SD	CV
Asteriscus	50	39.7	3.2	8.0
Sagitta	50	25.0	4.6	18.6
Lapillus	50	21.0	5.5	26.3

determined by examination of the age series of larvae, indicating that rings were indeed formed daily, and all rings were visible. Therefore, we assumed that rings were also formed daily in the lapillus and that underestimation of age was due to the inability to observe rings of low contrast in the opaque nuclear area rather than to other possibilities that have been reported, i.e. nondaily ring formation due to poor growth in herring, *Clupea harengus*, and turbot, *Scophthalmus maximus* (Geffen, 1982), and to ring spacing below the resolution limit of light microscopy in striped bass, *Morone saxatilis*, under suboptimal feeding regimes (Jones and Brothers, 1987).

Peters and McMichael (1987) had difficulty distinguishing the innermost rings in sagittae of some juveniles, and they developed an ageing method that did not require counting these rings. This method utilized transverse sections of larval sagittae in which rings were clearly visible to determine the distance from the primordium to the tenth ring. Subsequent juvenile ring counts were initiated at this distance away from the primordium. We also encountered difficulty in detecting all the rings near primordia in sagittae (and lapilli as well) due to the opacity of the nuclear region of the otoliths, but all rings were usually clearly visible in asterisci. Peters and McMichael (1987) made relatively accurate ring counts beyond the tenth ring on sagittae of 21-day-old known-age fish. However, we were not able to duplicate their success using our technique, because our counts underestimated the true age of 46-day-old fish by 21 days with a coefficient of variation of 18.6%. Duplicating their glycerin soaking technique did not improve our ring detection capability. The principle difference between our method and that of Peters and McMichael (1987) was the sectioning plane; they used the transverse plane, whereas we used the sagittal plane.

Because the otoliths were birefringent, they were easily observed within larval fish when illuminated with transmitted light between crossed polaroids. Sagittae and lapilli were easily seen in fish as small as 1.3 mm SL, whereas asterisci were observed in all fish greater than 3.0 mm SL. Comyns et al. (1989) detected two rings in sagittae and lapilli of larvae 2 days after fertilization (1 day posthatch), demonstrating that sagittae and lapilli are present at hatching; according to their growth curve, fish 3.0 mm SL were approximately 6 days old. Whereas the size at hatch was relatively constant, growth varied considerably with temperature, but the variation was not significant until the fish attain 4.0 mm SL (Comyns et al., 1989). Changes in growth rates due to water temperature are therefore not likely to have a significant effect on our estimate of age at asteriscus formation. Others have reported asteriscus formation at similar ages, e.g. at age 6 days in the Japanese eel, *Anguilla japonica* (Umezawa et al., 1989).

The asteriscus provided the most accurate estimate of age for juvenile red drum because it underestimated true age by only 6 days compared with 21 days for the sagitta and 25 days for the lapillus. The asteriscus ages were also the most precise, because the coefficient of variation was only 8.0% compared with 18.6 and 26.3% for the sagitta and lapillus respectively. Most of the variance in age estimates for all three otoliths was caused by the inability to resolve rings near the primordium and at the margin. Rings in the mid portion of asteriscus sections were consistent in shape, increment width, and clarity; a dominant, consistently identifiable, first ring was visible at the edge of the primordium.

The sagitta provided the next most accurate and precise estimates. Ages were underestimated by 21 days on average, and rings near the primordia were difficult to distinguish, resulting in a coefficient of variation more than a factor of two higher than that of the asteriscus. Because sagittae were present at hatching and early rings were detectable in smaller and younger fish (Peters and McMichael, 1987; Comyns et al., 1989), better accuracy and precision of ageing using sagittae may be possible with improvements in preparation and processing of the otolith. However, the Spurr mounting technique (Haake et al., 1982) used by Peters and McMichael (1987) and Comyns et al. (1989) can require several days for proper dehydration, curing, sectioning, and polishing whereas our polymer method required less than one hour to produce ground and polished slides from whole fish, thus allowing considerably more fish to be processed in comparable time periods.

Ages estimated from the lapillus were least accurate and precise because of poor clarity of rings near the primordia and because of the formation and fusion of numerous accessory primordia. This fusion of accessory primordia resulted in superimposition of rings near the margin and the presence of several planes of growth being visible in the same focal plane.

Although additional preparation may have increased resolution of rings near the primordia, poor ring resolution caused by accessory primordia would probably not have been improved.

The addition of a constant to asterisci ring counts (6 days) adjusted for the time lag between hatching and otolith formation and was not used to compensate for uncounted rings. The addition of constants to estimates of age did not affect the rank of the coefficients of variation.

All otolith diameters, especially sagittae, exhibited a strong correlation with fish lengths. This relation can be useful in backcalculating size at age. However, because the ring count did not accurately estimate age, accurate ages derived from sagittae can not be associated with back-calculated sizes. The relation between asteriscus diameter and fish length was not as strong as with sagittae, but the improvements in accuracy and precision in estimating age would increase the confidence in back-calculated sizes at age. However, because asterisci were not present at hatching, size-at-age information for fish <7 days old could not be backcalculated. Rings formed in the asteriscus were concentric and proportionally spaced throughout the otolith because no accessory primordia were formed, making it straightforward to measure radii or increment widths precisely regardless of the chosen axis of measurement.

We conclude that the asteriscus is the best structure to use in ageing young red drum >4.0 mm SL. Using our sagittal section technique with juveniles, we found that the asterisci clearly provided superior accuracy and precision in ageing. Previous efforts by Peters and McMichael (1987) to age juvenile red drum using transverse sections of sagittae provided reasonable age estimates; however, because they began counts a standard distance from the primordium to allow for uncounted rings (10), the accuracy and precision of resulting counts on 21-day-old fish cannot be known in the same sense that we estimated these statistics when all rings were counted on asterisci of 46-day-old fish. The advantage of using asterisci is that clear rings can be seen in sagittal sections, and grinding asterisci in the sagittal plane can be done relatively quickly. Furthermore, all rings were visible in the asteriscus, and only adjustment for age at formation was required to estimate true age.

Literature cited

Arnold, C. R.
1988. Controlled year-round spawning of red drum *Sciaenops ocellatus* in captivity. Contrib. Mar. Sci. Supp. to Vol. 50:65–70.

Bailey, K. M., and C. L. Stehr.
1988. The effects of feeding periodicity and ration on the rate of increment formation in otoliths of larval walleye pollock *Theragra chalcogramma* (Pallas). J. Exp. Mar. Biol. Ecol. 122:147–161.

Blaxter, J. H. S.
1971. Feeding and condition of Clyde herring larvae. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 160:128–136.

Brothers, E. B., and W. N. McFarland.
1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts (*Haemulon flavolineatum*). Rapp. P.-v. Réun. Cons. int. Explor. Mer 178: 369–374.

Brothers, E. B., E. D. Prince, and D. W. Lee.
1983. Age and growth of young-of-the-year bluefin tuna, *Thunnus thynnus*, from otolith microstructure. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:49–59.

Campana, S. E., and J. D. Neilson.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 44:1014–1032.

Comyns, B. H., J. Lyczkowski-Shultz, C. F. Rakocinski, and J. P. Steen Jr.
1989. Age and growth of red drum larvae in the North-Central Gulf of Mexico. Trans. Am. Fish. Soc. 118:159–167.

Comyns, B. H., J. Lyczkowski-Shultz, D. E. Neiland, and C. A. Wilson.
1991. Reproduction of red drum, *Sciaenops ocellatus*, in the north-central Gulf of Mexico: seasonality and spawning biomass. *In* R. D. Hoyt (ed.), Larval fish recruitment and research in the Americas: proceedings of the thirteen annual larval fish conference; Merida, Mexico, May 1989, p. 17–26. NOAA Tech. Rep. NMFS 95.

David, A. W., and J. H. Paul.
1989. Enumeration and sizing of aquatic bacteria by use of a silicon-intensified target camera-linked image-analysis system. J. Microbiol. Methods 9(4):257–266.

Fuiman, L. A., and D. R. Ottey.
1993. Temperature effects on spontaneous behavior of larval and juvenile red drum, *Sciaenops ocellatus*, and implications for foraging. Fish. Bull. 91:23–35.

Geffen, A. J.
1982. Otolith ring deposition in relation to growth rate in herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. Mar. Biol. 71:317–326.

Haake, P. W., C. A. Wilson, and J. M. Dean.
1982. A technique for the examination of otoliths by SEM with application to larval fishes. *In* C. F. Bryan, J. V. Conner, and F. M. Truesdale (eds.) Proceedings of the fifth annual larval fish conference, p. 12–15. LSU Press, Baton Rouge, LA.

Hay, D. E.
1982. Fixation shrinkage of herring larvae: effects

of salinity, formalin concentration, and other factors. Can. J. Fish. Aquat. Sci. 39:1138–1143.

Holt, S. A., C. L. Kitting, and C. R. Arnold.
1983. Distribution of young red drum among different sea-grass meadows. Trans. Am. Fish. Soc. 112:267–271.

Irie, T.
1960. The growth of the fish otolith. J. Fac. Fish. Anim. Husb. Hiroshima Univ. 3(1):203–221.

Jones, C.
1986. Determining age of larval fish with the otolith increment technique. Fish. Bull. 84:91–103.

Jones, C., and E. B. Brothers.
1987. Validation of the otolith increment ageing technique for striped bass, *Morone saxatilis*, larvae under suboptimal feeding conditions. Fish. Bull. 85:171–178.

Leak, J. C.
1986. The relationship of standard length and otolith diameter in larval bay anchovy, *Anchoa mitchilli* (Val.): a shrinkage estimator. J. Exp. Mar. Biol. Ecol. 95:167–172.

Mercer, L. P.
1984. A biological and fisheries profile of red drum, *Sciaenops ocellatus*. N.C. Dep. Nat. Res. Comm. Devel., Div. Mar. Fish., Spec. Sci. Rep. 41, 89 p.

Panella, G.
1971. Fish otoliths: daily growth layers and periodical patterns. Science (Washington, D.C.) 173:1124–1127.

Peters, K. M., and R. H. McMichael Jr.
1987. Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. Estuaries 10:92–107.

Radke, R. L.
1989. Larval fish age, growth, and body shrinkage: information available from otoliths. Can. J. Fish. Aquat. Sci. 46:1884–1894.

Theilacker, G. H., and K. Dorsey.
1980. Larval fish diversity, a summary of laboratory and field research. *In* G. D. Sharp (ed.), Workshop on the effects of environmental variation on the survival of larval pelagic fishes, p. 105–142. FAO, Intergov. Oceanogr. Comm., Workshop Rep. 28.

Umezawa, A., K. Tsukamoto, O. Tabeta, and H. Yamakawa.
1989. Daily growth increments in the larval otolith of the Japanese eel, *Anguilla japonica*. Jpn. J. Ichthyol. 35(4):440–444.

Abstract.—Squirrelfish of the genus *Myripristis* are valued in small-scale fisheries throughout much of the tropics. The life history and species biology of most of these soldierfishes is poorly known. For the brick soldierfish, *M. amaena*, in Hawaii and Johnston Atoll, we found that sexual maturity for both sexes was reached between 145 and 160 mm standard length at about six years of age — a large fraction of the apparent maximum size and lifespan. Fecundity was relatively low and increased as the fifth power of body weight. Spawning peaked from about early April to early May, and a secondary peak occurred in September. *Myripristis amaena* is a nocturnal predator, feeding mostly on meroplankton, especially brachyuran crab megalops, hermit crab larvae, and shrimps, but also taking a variety of benthic prey. In pristine fish communities, holocentrids were abundant, quantitatively important (often dominant) reef predators and prey. *Myripristis amaena* (and probably other common and important soldierfish) seems to be relatively long lived (at least 14 years), slow growing, and late maturing. The populations suffer considerable natural predation and depend mainly on the largest and oldest fish for reproduction. Heavy, unregulated fishing of these soldierfish, especially at prereproductive size, may severely reduce populations.

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Reproductive and trophic ecology of the soldierfish *Myripristis amaena* in tropical fisheries

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Soldierfish, Myripristinae, of the squirrelfish family, Holocentridae, occur widely throughout the tropics (Greenfield, 1965, 1968, 1974). They are typically abundant and are an important component of commercial, recreational, and subsistence fisheries in much of the world's tropics. Throughout most of the central and western Pacific Ocean, the brick soldierfish, *Myripristis amaena* (Castlenau), is an important member of this group (Greenfield, 1968). It contributes significantly to fish communities and to fishery catches in shallow reef and rocky habitats. It is particularly important in the recreational fishery at Johnston Atoll (JA), where it is typically the species caught in greatest abundance (Irons et al.[1]). It is also common in catches throughout the Hawaiian archipelago.

Relatively little quantitative information has been published about the life history and biology of species of the genus *Myripristis*, and very little is available about *M. amaena* in particular. Data about diets are available for only a few species of *Myripristis*; for most of these, sample sizes are small (e.g. 14 specimens for *M. amaena*; Hobson, 1974). Results on age and growth from our studies of the JA population of *M. amaena* have been reported (Dee and Radtke, 1989). There have been no thorough published studies of the reproduction of *M. amaena* or closely related species. Because of the wide distribution, considerable abundance, and substantial fishery importance of *M. amaena*, we undertook to describe more fully its food requirements and trophic position in the community and to quantify the reproductive characteristics that affect the dynamics of its populations. The parameters we determined may also provide reasonable first approximations for similar *Myripristis* species that are less well studied. The results will contribute to an informed approach to management of species that are now typically unmanaged and probably overfished in most localities with even moderately dense human populations.

The JA population of *M. amaena* was the major focus of this study for several reasons. Many biological and ecological characteristics of *M. amaena* (e.g. size, morphology, habits, habitat used, fishery value) seem to be representative of a num-

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[1] Irons, D. K., R. K. Kosaki, and J. D. Parrish. 1990. Johnston Atoll resource survey. Final report of Phase Six (21 July 1989–20 July 1990). Project rep. to U.S. Army Engineer Distsrict, Honolulu, HI, 150 p.

ber of common soldierfish species. Johnston Atoll provided a logistically good base for study, where *M. amaena* was the dominant *Myripristis* species, with populations not seriously depressed by fishing. The species was plentiful and easily collected at many locations throughout the year, and a good range of sizes was readily available. The importance of *M. amaena* in the fishery at JA facilitated collection of specimens and fishery data.

Materials and methods

Specimen collection and handling

Most specimens used in all analyses were taken at Johnston Atoll, a remote, coral-rich, oceanic pinnacle about 1250 km SW of Honolulu (Halstead and Bunker, 1954; Amerson and Shelton, 1976; Randall et al., 1985; Maragos and Jokiel, 1986). Smaller collections were made from a rich, fringing coral reef tract at Puako in South Kohala on the leeward coast of Hawaii Island (Hayes et al., 1982). A few specimens were collected from the almost uninhabited Northwestern Hawaiian Islands (NWHI), primarily from shallow, coralline areas at French Frigate Shoals and Midway (located about 750 and 2000 km, respectively, northwest of Honolulu).

Specimens from all three locations contributed to size–frequency analysis, visual assessment of gonad condition (maturity), and analysis of gut contents. At JA and Puako, gonad weight was taken to determine reproductive season and size at first reproduction; at JA, gonad samples were preserved for histological examination and estimation of fecundity.

Most specimens at all locations were collected from shallow waters (<15 m). The major methods of collection were spearing, bait casting with a line, and some spot applications of ichthyocide. At JA, we collected specimens from several sites inside the lagoon and just outside the barrier reef. Collections and extensive underwater observations were made at frequent intervals between February 1984 and January 1986. Sampling was less intensive in some months because of constraints on travel to JA. At Puako and in the NWHI, specimens were collected rather widely within coralline habitats. At Puako, about half the specimens were collected as quickly as feasible (May–June 1981), once the species was found to be in reproductive season. Other collections there were distributed throughout the year. In the NWHI, specimens were collected in March, April, May, August, and November.

Standard (SL), fork (FL), and total (TL) lengths of all captured specimens were measured to the nearest millimeter, and weights were taken to the nearest 0.1 g. (Appendix A provides functions, fitted by regression, to convert between SL, FL, and TL.) Whole guts and gonads were excised and preserved in 10% buffered formalin for further analysis. Some specimens were frozen whole and stored for some weeks or months before processing.

Source of size–frequency data

At JA, Puako, and the NWHI, length and weight data from all specimens collected for other purposes were available for size-frequency estimation. In addition, at JA, creel census data were obtained from fishermen's catches on many days over the period of study. Fish landed by boat and shore fishermen were examined, and each specimen was measured and weighed as above. These data provided a much larger and possibly more representative sample than our collections alone.

Feeding

The volume of each complete gut specimen was measured by displacement of water before and after the gut was opened and all contents removed. The total volume of contents was determined by difference. All diet items were sorted into systematic categories and identified to the lowest possible taxa. For each prey category, the number of individuals, length, extent of digestion, location in gut, and volume were recorded. Whole reference specimens were used as an aid in identifying prey items and estimating the original size of the prey by comparison of the dimensions of recognizable parts. Volume of remains in each prey category was estimated by displacement of water (Wolfert and Miller, 1978).

A measure of overall importance of each prey category was calculated by using the Index of Relative Importance (IRI), as defined by Pinkas et al. (1971):

$$\text{IRI} = \text{frequency } \% \times (\text{numerical } \% + \text{volume } \%),$$

where frequency % = (the number of guts containing prey of one category divided by the total number of guts that contained any identifiable prey) × 100;

numerical % = (the number of individuals of one prey category divided by the total number of prey individuals found in all the guts) × 100;

and volume % = (the volume of one prey category divided by the total volume of all prey found in the guts) × 100.

Reproduction

Gonads of 430 specimens from JA were visually examined macroscopically and classified (based on their size, color, texture, and morphology) as male, female, immature, or unknown. A subsample of these gonads from specimens collected during probable reproductive and nonreproductive periods was removed, wet weighed to the nearest 0.001 g, and preserved in 70% isopropyl alcohol for further examination. Gonads selected for histology were prepared and embedded by using Kahles solution (Guyer, 1953, p. 236) with a graded series of ethyl alcohol and butyl alcohol dehydration. Embedded subsamples taken from the anterior, middle, and posterior regions of the selected gonads were then sectioned at 5 and 10 μm, mounted on plain microscope slides, and stained by using Delafield hematoxylin and eosin Y techniques (Humason, 1979, p. 112, 119–123).

Size at first reproduction (SFR) was estimated based on visual examination of gonads and by using the gonadosomatic index (GSI), where:

$$GSI = (\text{gonad wet weight}/\text{whole body wet weight}) \times 100.$$

The GSI was plotted against SL for male and female *M. amaena* collected from periods during which the species seemed to be reproductively active. A sharp rise in the GSI at some length indicated the SFR. The SFR was also estimated based on histological examination of gonads from specimens collected during the April 1984 spawning peak. Eggs were examined for size and stage of development from sections of 11 females representing a range of sizes. Staging was based on size, morphology, and staining properties of eggs (Khoo, 1978; Wallace and Selman, 1981). Testes from five males were examined histologically for presence of sperm.

Spawning season was estimated by plotting GSI against month of capture for 99 sexually mature males and females (larger than 145 mm SL) collected throughout the sampling period. Histological sections of samples from March, April, May, July, and August 1984 were examined for further validation of reproductive periods.

We did not identify individual clutches of ova in females. Based on the histology, we identified ova ≥0.4 mm on the major axis as being in an advanced stage of yolk development and defined this stage as mature (Table 1, See Fig. 3). Our fecundity value is an estimate of the number of such ova in a female specimen. Ovaries from 12 gravid females collected at JA during the January 1986 spawning peak were used to estimate fecundity. Three 0.02-g aliquots were taken from the midsection of each ovary. All mature ova (≥0.4 mm on the major axis) were counted with the aid of a binocular dissecting microscope. Fecundity, F, was estimated for each female from the formula:

$$F = ((N_1+N_2+N_3)/3) \times (G/A),$$

where N_1, N_2, N_3 = the number of mature ova in each aliquot;

G = total gonad weight (g);
A = weight of a gonad aliquot (0.02 g).

For specimens from Puako, the same procedures were followed except that no histological preparation or examination was done, and ripeness was estimated simply on the basis of visual appearance of

Table 1

Stages of development of oocytes in the brick soldierfish, *Myripristis amaena* (also see Fig 3).

Stage	Oocyte diameter (mm)	Description
oogonia and primary growth	0.01–0.04	scant cytoplasm; centrally located nucleus; single large nucleolus; stains dark red
perinuclear	0.04–0.056	multiple nucleoli around inner side of nuclear membrane; stains dark purple
secondary growth and yolk vesicle	0.056–0.14	clear-staining cortical alveoli begin as ring at cytoplasm periphery, then increase in size and occupy whole cytoplasm
yolk granule	0.14–0.40	true vitellogenesis; red-staining yolk granules begin to form around cytoplasm periphery (early vitellogenesis) then increase in size and occupy whole cytoplasm (late vitellogenesis); zona radiata first appears
maturation	0.40–0.54	yolk granules fuse into yolk "plates" which stain light blue; fusion begins at center and spreads throughout cytoplasm

the gonad and GSI. The SFR, but not spawning season, was estimated quantitatively by using these measures. Egg sizes were not measured, and fecundity was not estimated.

Results

Feeding

Guts from 64 specimens collected at JA at night contained identifiable prey items (Table 2). Crab larvae dominated the diet, producing much larger IRI values than any other major systematic group (Table 3). Brachyuran megalops (mostly Portunidae) were found in over 90% of the analyzed guts. Despite their relatively small size, they were important in volume (28%) as well as numbers (38%). Hermit crab larvae (Paguroidea) were present in over half the guts, and alpheid shrimp in slightly less than half. Both these groups provided significant fractions of all prey numbers and volume and had large IRI values; hermit

Table 2

Diet of *Myripristis amaena* based on 64 specimens from Johnston Atoll, 9 from the Northwestern Hawaiian Islands, and 22 from Puako, Hawaii Island. Results reported by Hobson (1974) based on 14 specimens from Kona, Hawaii Island, are also included for comparison. Table shows the percent of predator individuals that consumed each prey (F), and the percent of all numbers (N) and volume (V) provided by each prey. Values for the highest systematic levels are printed in bold. (See Table 3 for Indices of Relative Importance for these highest level groups.)

	Numerical percent[1]			Volume percent[1]				Frequency percent			
						Hawaii Island				Hawaii Island	
Prey category	Johnston Atoll	N.W. Hawaiian Islands	Puako (Hawaii Island)	Johnston Atoll	N.W. Hawaiian Islands	Puako	Kona[2]	Johnston Atoll	N.W. Hawaiian Islands	Puako	Kona[2]
Crabs[3]	**60.8**	**33.3**	**71.2**	**50.3**	**8.4**	**35.0**	**75.1**	**100**	**11.1**	**68.2**	**100.0**
Portunidae	37.8			27.6				90.6			
Paguroidea (hermit crab)	23.0		0.3	22.7		[4]		59.4		4.6	
Galatheidae			8.5			7.7				4.6	
Shrimp	**11.8**	**22.2**	**11.4**	**10.8**	**8.4**	**>2.0**	**9.3**	**46.9**	**11.1**	**27.3**	**28.6**
Alpheidae	11.8		3.5	10.8		0.4		46.9		13.6	
Palaemonidae			2.0			0.6				13.6	
Hippolytidae			3.0			>0.8				13.6	
Caridea unidentified			0.6			[4]				4.6	
Shrimp larvae			0.9			[4]				4.6	
Shrimp unidentified			1.5			0.2				4.6	
Stomatopods	**1.6**	**11.1**	**4.1**	**6.7**	**8.4**	**6.5**	**0.1**	**37.5**	**11.1**	**22.7**	**7.1**
Lobsters	**0.06**		**0.9**	[4]		**21.5**		**3.1**		**13.6**	
Polychaetes	**12.0**		**0.3**	**15.3**		**0.4**	**0.4**	**70**[5]		**4.6**	**7.1**
Eunicidae	6.7			11.7				60[5]			
Nematonereis sp.	6.3			2.8				59.4			
Eunice sp.	0.4			8.9				9.4			
Opheliidae (*Polyophthalmus* sp.)	5.3			3.6				43.8			
Fish	**2.4**	**33.3**	**1.8**	**10.5**	**33.6**	**5.8**	**2.9**	**32**[5]	**22.2**	**22.7**	**21.4**
Eels, unidentified	2.2			8.5				21.9			
Mysids	**5.9**		**0.3**	**4.3**		[4]	**0.3**	**18.8**		**4.6**	**28.6**
Amphipods	**0.1**		**5.0**	**0.1**		**>0.2**	**0.2**	**9.4**		**18.2**	**7.1**
Gammaridea			4.7			0.2	0.2			13.6	7.1
Tanaids	**5.4**			**2.0**				**50.0**			
Copepods			**1.2**			[4]	**0.1**			**9.1**	**7.1**
Isopods							**0.1**				**7.1**
Cephalopods			**0.3**			**1.5**	**1.4**			**4.6**	**7.1**
Octopus sp.			0.3			1.5				4.6	
Gastropods			**3.5**			**1.4**	**0.4**			**22.7**	**14.3**
Crustacean parts, unidentified		[6]	[6]		**41.2**	**25.8**	**9.7**		**66.7**	**77.3**	**57.1**

[1] Data for unidentified crustacean parts are excluded from the calculation
[2] Data from Hobson (1974); numerical percents were not reported
[3] Larvae (mostly megalops), except those from the Northwestern Hawaiian Islands that were juvenile majids.
[4] Data are missing.
[5] Calculated from a subset of 31 specimens.
[6] Not countable

Table 3

Summary of the diet of *Myripristis amaena* at the highest systematic levels of prey. Results are shown as percents of the summed Index of Relative Importance (IRI). (See Table 2 for details at these and other systematic levels.)

Prey category	Johnston Atoll (n=64)	Northwestern Hawaiian Islands (n=9)	Puako (Hawaii Island) (n=22)
Crabs	72.3	18.5	84.8
Shrimp	6.9	13.6	4.3
Stomatopods	2.0	8.6	2.8
Lobsters	[1]		3.6
Polychaetes	12.4		0.04
Fish	2.7	59.3	2.0
Mysids	1.2		[1]
Amphipods	0.01		1.1
Tanaids	2.4		
Cephalopods			0.1
Gastropods			1.3
Crustacean parts, unidentified	Few[2]	Very many[2]	Very many[2]

[1] Data are missing.
[2] Not countable; not included in computation of IRI.

crabs were more important by all measures. Two *M. amaena* specimens contained a total of three lobsters. Fish were moderately important prey by frequency and volume. Many prey specimens appeared to be eels, probably mostly ophichthids. Polychaetes were the most important benthic prey, present in about 70% of all fish and providing over 10% of all prey by numbers and volume.

Twenty-two specimens from Puako contained prey identifiable to some level (Table 2). Nearly 70% of these contained crab megalops larvae; a hermit crab was identified in one of these and a galatheid crab, *Galathea spinosorostris*, in another. Crab larvae were also the major prey in numbers (over 70%) and volume (35%) and were strongly dominant in the IRI (Table 3.). Shrimp were eaten by the second largest number of fish (nearly 30%) and were second in importance numerically (over 10%), but minor in volume. They were far less an important prey at Puako than at JA, and were more evenly divided among Alpheidae, Palaemonidae, and Hippolytidae (including two *Saron marmoratus*). Lobsters (three individuals) appeared in only three guts (14%), but they accounted for over 20% of total prey volume. Both the slipper lobster, *Scyllarides squammosus*, and the Hawaiian clawed lobster, *Enoplometopus occidentalis*, were eaten. No other groups made major individual contributions to the diet. However, stomatopods and fish accounted for at least several percent of the number of consumers (frequency %) and volume. One octopus appeared in the diet at Puako. Benthic prey included at least a few percent gastropods (by the various measures) and a polychaete specimen. Nearly 80% of all fish also contained some quantity of unidentifiable crustacean parts, which accounted for over 25% of the total prey volume. Calculated as a percent of only the total prey identifiable to more specific groups, the volume % of each of those groups was considerably higher.

Only nine specimens from the NWHI contained prey identifiable to any level (Table 2). The total amount of prey recovered was small. Fish (including at least one pomacentrid), shrimp, juvenile crabs (including majids), and stomatopods were found in one or two guts each in total numbers of one to three individuals each. Six guts contained unidentifiable crustacean parts, which accounted for over 40% of the total diet volume. Fish were next in volume, and the other three groups contributed little volume.

At all three locations, the diet of *M. amaena* was heavily dominated by small juvenile stages of crustacean species that become much larger as adults. These prey included all the major groups of large crustaceans that are dominant in the diets of many demersal species of reef fishes studied in Hawaii (Parrish et al., 1985). Besides the crab and shrimp prey — quantitatively important in the diet of *M. amaena* at all three locations — stomatopods were eaten at all locations, and were the dominant prey of the Myripristinae generally in the NWHI (Parrish, unpubl. data). *Pseudosquilla oculata* was a stomatopod species identified in our *M. amaena* specimens that also was prominent in the diets of other Myripristinae and other demersal reef fishes in our studies in Hawaii.

Small peracaridan crustaceans were conspicuous in the diet at JA (Table 2). Mysids and tanaids were present in the gut contents of many fish specimens, and each group contributed a few percent of the total number and volume of prey. Only one individual of each was identified at Puako. Amphipods were somewhat less widely found as diet components at JA and their abundance was trivial. At Puako they were present in about 18% of the fish and made up about 5% of numbers but were trivial in volume. Most of those identified were gammarids. A few isopods were found in JA specimens, and traces of copepods were found in Puako specimens. More peracaridans and other small crustaceans were very likely part of the residue of unidentifiable crustacean parts that appeared widely at all locations.

Myripristis amaena showed the expected strongly nocturnal feeding habit. At JA, guts from all 64 speci-

mens taken between 2000 and 0200 hours contained identifiable prey items. From 62 guts collected in the daytime, only four (taken at 0730 hours) contained more than one identifiable food item. At Puako, all 11 guts collected between 2300 and 0930 hours contained identifiable prey items, all of which might reasonably be the result of night or dawn feeding. Eleven specimens taken between 1000 and 1300 hours contained some food, much of it only unidentified crustacean parts. Sixteen specimens collected between 1100 and 1500 hours contained no identifiable prey. Of 61 specimens from the NWHI, only nine (collected between 0800 and 1100 hours) contained identifiable prey, mostly considerably digested. The remaining 52 specimens, collected between 1000 and 1600 hours, were empty or contained well digested, unidentifiable material.

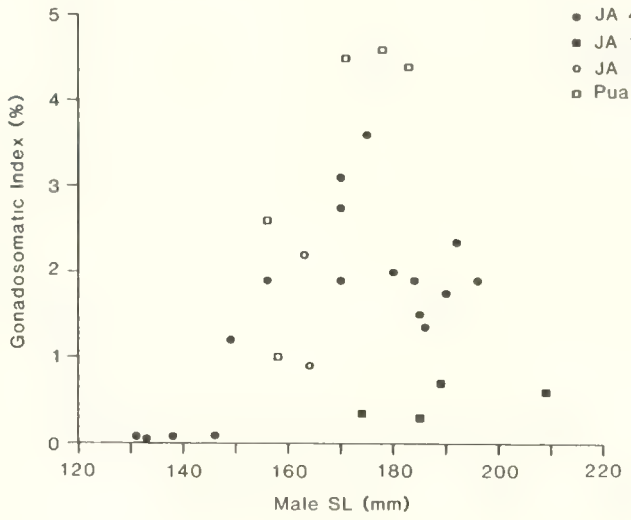

Figure 2

Values of gonadosomatic index and corresponding standard length for male brick soldierfish, *Myripristis amaena*, collected during reproductive peaks at Johnston Atoll (JA) and Puako, Hawaii.

Reproduction

The GSI of each sex collected during reproductive periods throughout the year from JA and Puako combined indicated an increase in the range of 153–156 mm SL for females (Fig. 1) and in the range of 149–156 mm SL for males (Fig. 2). Based on histological examination of developing oocytes in JA females, five developmental stages were identified (Table 1). Sexual maturity was defined based on the presence of ovaries with oocytes in the late yolk granule stage for females (≥0.4 mm diameter; see Fig. 3) and on the presence of mature sperm in males (Fig. 4). The 11 ovaries and five testes examined histologically indicated that first sexual maturity occurred near 154 mm SL for females and 149 mm SL for males. The results were consistent with those from visual examination of 24 total gonads (males and females) from Puako.

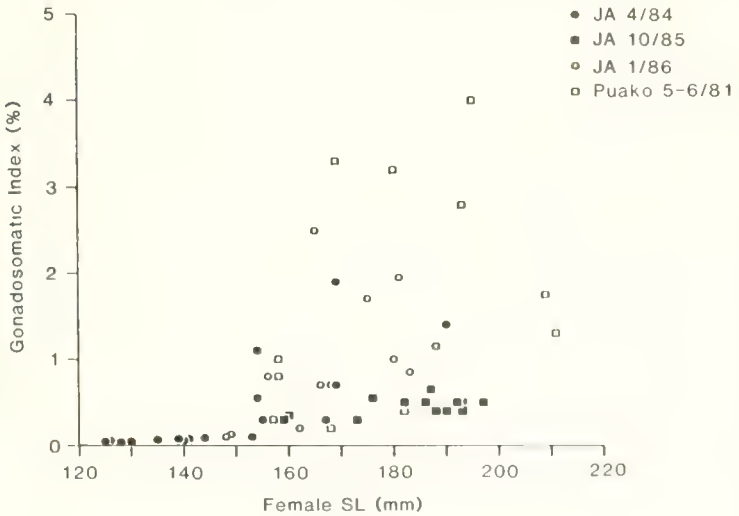

Figure 1

Values of gonadosomatic index and corresponding standard length for female brick soldierfish, *Myripristis amaena*, collected during reproductive peaks at Johnston Atoll (JA) and Puako, Hawaii.

When GSI of mature specimens (larger than 145 mm SL) from JA was plotted against month of capture, with data from all months except September, spawning peaks were discernible in January, April, May, and October; the major peak was in April (Fig. 5). Based on visual examination, GSI, and histology, no gravid individuals were recorded among specimens collected during any other month. (Samples were rather small in some months.)

The fecundity estimated from the 12 ovaries sampled at JA ranged from 12,400 mature ova for a 156-mm SL fish to 69,200 for a 181-mm SL fish (Appendix B). Regressions were performed with fecundity, F, in number of mature eggs as a function of standard length, SL, in millimeters, and alternatively as a function of whole wet body weight, W, in grams. The fit was

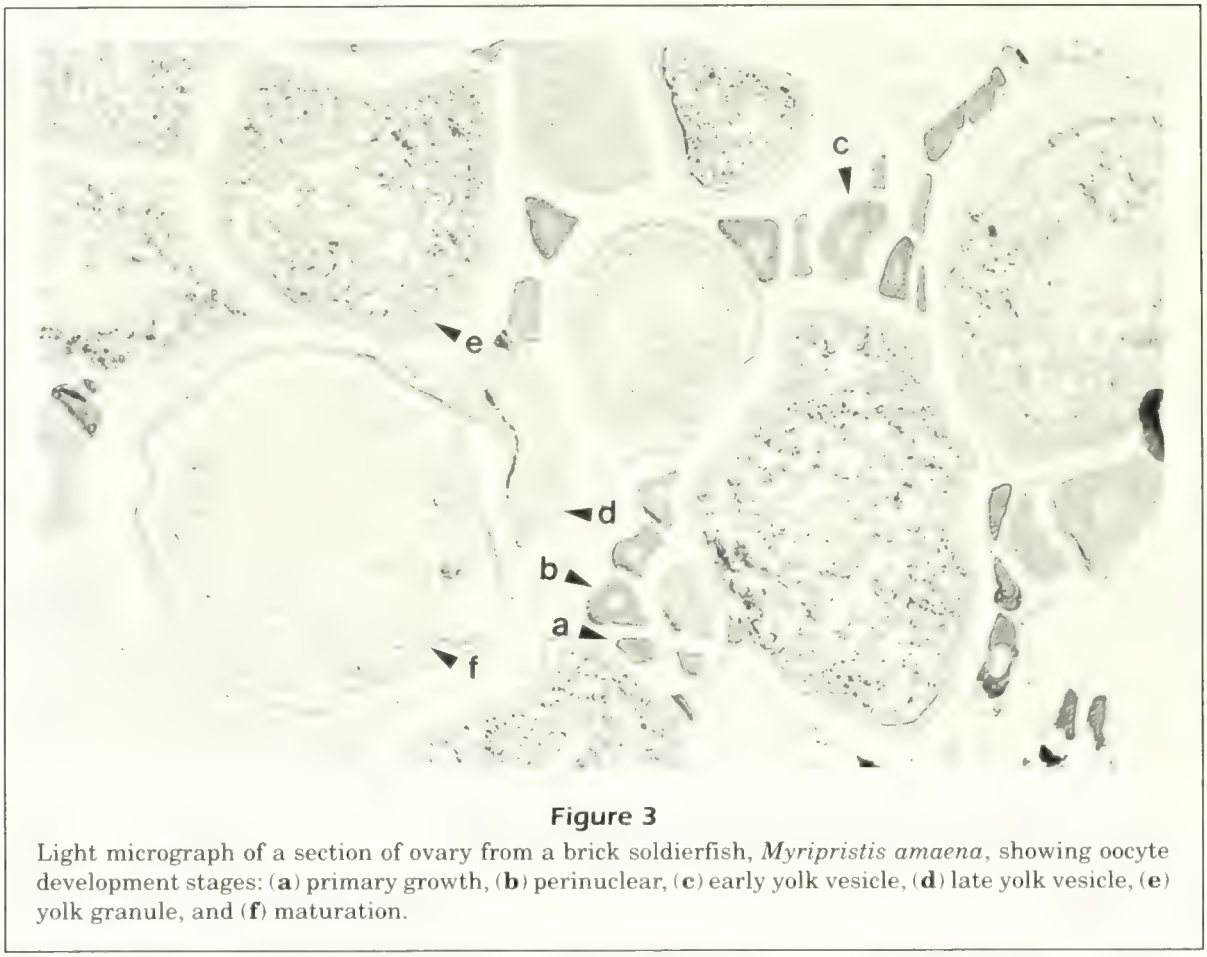

Figure 3

Light micrograph of a section of ovary from a brick soldierfish, *Myripristis amaena*, showing oocyte development stages: (**a**) primary growth, (**b**) perinuclear, (**c**) early yolk vesicle, (**d**) late yolk vesicle, (**e**) yolk granule, and (**f**) maturation.

slightly better for power functions than for linear functions in both cases:

$$F = 5.029 \times 10^{-20}(\mathrm{SL})^{10.614}, \qquad r^2 = 0.75$$
$$F = 1.447 \times 10^{-7} W^{5.0038}, \qquad r^2 = 0.86 \quad \text{(Fig. 6)}.$$

Based on the weight-frequency distribution of the recreational catch sampled at JA (Fig. 7A) and our weight-fecundity expression, in an average year, the reproductive output of the population is distributed as shown in Figure 7C. Thus, for example, about 54% of all eggs are produced by fish of 250 g and larger (over 13 years old) — the oldest 20% of the population. Weight classes between 200 and 250 g (ages of about 10 to 13 years) constitute about 38% of the reproductive population and produce about 35% of all eggs. Smaller fish — over 41% of the reproductive population — produce only about 11% of all eggs. Fishing pressure (all recreational) is light at JA, and many large fish remain.

Discussion

Feeding

With the possible exception of some of the larger shrimp and stomatopod specimens, the dominant prey found in our *M. amaena* samples at all three locations were in some sense planktonic. The large number of crab, shrimp, and stomatopod larvae eaten, as well as the presence of prey such as copepods and mysids, strongly indicates that *M. amaena* does much of its feeding in the water column. Hobson (1974) found generally the same prey groups dominant and concluded that *M. amaena*, *M. berndti*, and *M. kuntee* were planktivores at Kona on Hawaii Island. A similar suite of prey items found in *M. kuntee* at Puako in the present work and at Oahu (Oda and Parrish, 1982) indicated that zooplankton were the dominant food source. Our diet studies of *M. berndti* at Puako show a similar result. Brecknock (1969) found that *M. berndti* was primarily zooplanktivorous at Oahu. The results of Harmelin-Vivien (1979) for *M. bowditchae* in Madagascar and of ter Kuile (1989) for *M. murdjan* in the Flores Sea indicate a large proportion of meroplanktonic prey in the diets. These soldierfishes seem morphologically adapted for picking small prey individuals from the water column (Hobson, 1972, 1974), and they have often been observed foraging extensively well above the bottom (Brecknock, 1969; Hobson, 1972, 1974).

Figure 4

Light micrograph of a section of testis from a brick soldierfish, *Myripristis amaena*. (**S**) indicates large pockets of mature sperm.

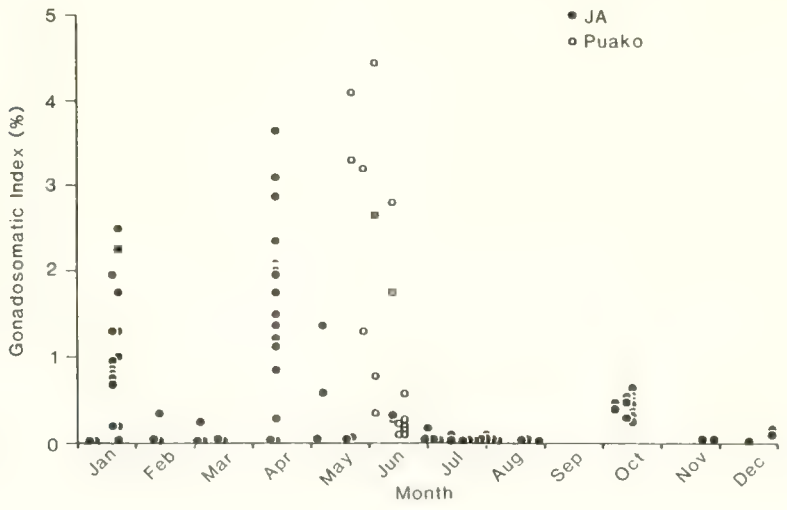

Figure 5

Values of gonadosomatic index and corresponding dates of capture for brick soldierfish, *Myripristis amaena*, collected at Johnston Atoll (JA) and Puako, Hawaii.

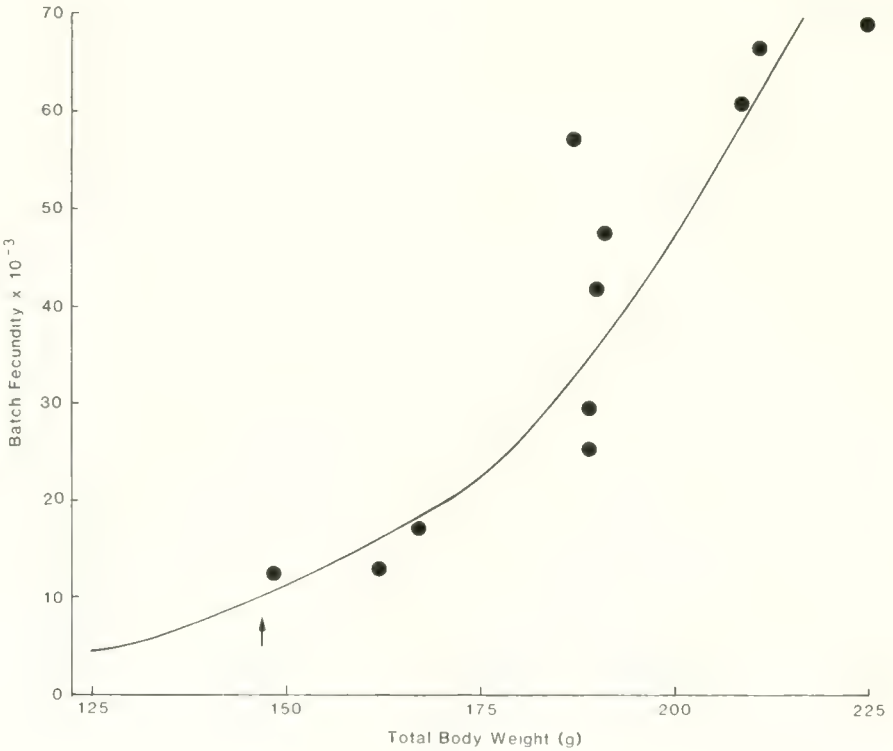

Figure 6

Batch fecundity estimate, F, and corresponding wet body weight, W, for ovaries of 12 brick soldierfish, *Myripristis amaena*, from Johnston Atoll (JA). The curve for the functional relationship fitted by regression is shown: $F = 1.447 \times 10^{-7}\ W^{5.0038}$.

A large fraction of all food eaten by *M. amaena* and most other *Myripristis* species appears to be taken from the water column, often at some distance above the substrate. However, relatively little of what we found or of what has been reported in the diets of these species in Hawaii appears to be holoplanktonic. Among the many small crustacean groups identified in the diets, few copepods were found. A number of the common crustacean prey were from groups such as mysids and amphipods that migrate vertically (often on a diel schedule) within shallow water, and may shelter on or near benthic substrate, within caves, cavities, rubble, or other cover during part of the day. Larval and young juvenile forms of larger benthic crustacea, such as crabs, lobsters, stomatopods, and some shrimp, may be components of this migrating "semiplankton." Some shrimps may be intermittently sedentary or free swimming as adults. What is known of this semiplankton (Alldredge and King, 1977; Porter and Porter, 1977; Parrish, 1989) and of the diet and feeding of *Myripristis* suggests that these squirrelfishes are not restricted to either planktonic or benthic feeding, but that they consume these prey groups wherever they are accessible.

The dominance of this semiplanktonic, probably vertically migrating, fauna in the diet of these fishes has important implications for their trophic linkage to the surrounding systems. Whatever the spatial and temporal details of their residence in the water column, the dominant "zooplankton" seem characteristic of an inshore aggregation, probably tied closely to shallow water. Therefore, these squirrelfishes depend for their trophic support largely on local sources of secondary production and possibly even primary nutrients (Parrish, 1989). This trophic arrangement is in contrast to the traditional concept of shallow-water planktivorous fishes supported by holoplankton of open ocean origin brought to the coast by prevailing oceanic currents.

There are reports of some *Myripristis* species feeding close over the substrate (Brecknock, 1969; ter Kuile, 1989). Hiatt and Strasburg (1960) noted that *M. microphthalmus* (=*violaceus*; Greenfield, 1974) in the Marshall Islands "takes a great variety of crustaceans which are associated with, or swim near, the coral mounds in which this...fish secludes itself." They also found that some of their specimens had eaten tube-dwelling polychaetes—clearly a benthic

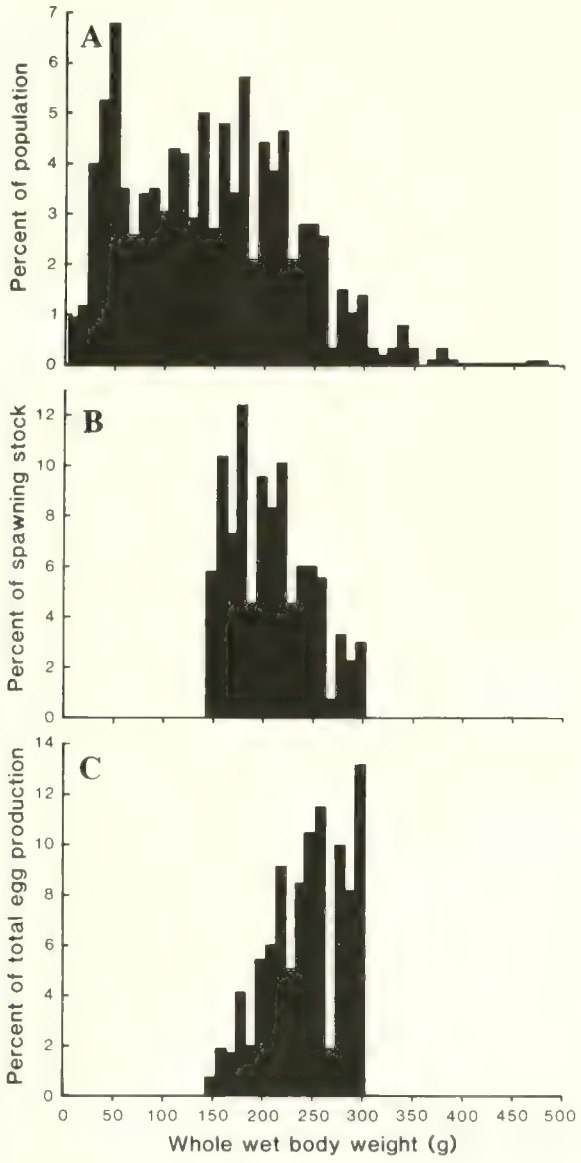

Figure 7

Size-frequency distribution of population numbers and population egg production of the brick soldierfish, *Myripristis amaena,* at Johnston Atoll (JA). (**A**) Distribution of whole wet body weights of all 855 specimens measured from recreational catches and scientific collections combined. (**B**) Distribution of wet weights of only the reproductively mature portion of the population up to 300 g (n=396). (**C**) Distribution of egg production by wet weight of spawners (n=396) based on the spawning population distribution in (B) and the fecundity vs body weight relationship developed from gonad samples. The fish population is arbitrarily truncated at 300 g for (B) and (C), which excludes 25 specimens distributed very irregularly over 18 weight classes, and with sizes much larger than those used to develop the size-fecundity relationship.

prey that was common in adjacent sandy patches. Harmelin-Vivien (1979) reported that polychaetes were the major prey by weight found in *M. bowditchae* (=*murdjan*; Randall and Gueze, 1981) in Madagascar, and she specifically noted that this fish sometimes fed on the bottom. Polychaetes were a minor prey of *M. berndti* at Oahu (Brecknock, 1969) and were fairly abundant in *M. murdjan* in the Flores Sea (ter Kuile, 1989). A polychaete was found in a *M. amaena* specimen from Kona (Hobson, 1974) and in one from our collections at Puako. In our JA collections, they were much more common and abundant, producing the second largest IRI value of the major systematic groups (Table 3). The JA taxa were Sedentaria, which must certainly have been benthic dwellers. At Puako, at least five of our 36 specimens of *M. berndti* and two of our 21 specimens of *M. kuntee* with prey contained polychaetes. Three specimens of *M. berndti* contained several polychaete individuals each.

Gastropods (presumably benthic species) were reported by Hobson (1974) in the diets of *M. amaena* and *M. berndti* from Kona. A benthic gastropod was found in the gut of a *M. berndti* at Puako, and they were fairly common in our *M. amaena* specimens there. Brecknock (1969) found a few gastropods in guts of *M. berndti* from Oahu and reported foraging by this species on the bottom of aquaria. One *M. berndti* specimen from Puako contained part of an arm of a bottom-living ophiuroid.

It seems clear that *M. amaena* and some other *Myripristis* species eat some fully benthic taxa. It is unlikely that such prey make up a major part of the diet for more than a very few *Myripristis* species. However, the ability of these squirrelfishes to employ this feeding mode enables them to exploit a greater range of food resources, at least on an opportunistic basis. Again, the trophic source seems to be local.

Trophic role of squirrelfishes in tropical communities

Holocentrids commonly make up a significant portion of the total natural fish community and are important predators throughout their range. In the uninhabited NWHI, nine species of holocentrids, including *M. amaena*, made up 4.5% of all individuals in the fish community (Norris and Parrish, 1988). In Tulear, Madagascar, three species of holocentrids represented 2.2% of the total fish population (Harmelin-Vivien, 1981). At JA, *M. amaena* alone provided about 2% of all individuals in the fish community. Together with three other species of holocentrids, it accounted for about 3% of the total fish community there (Dee et al.[2]).

[2] Dee, A. J., D. K. Irons, and J. D. Parrish. 1985. Johnston Atoll resource survey; a final report of the initial phase (19 Jan 1984–20 Jul 1985). Project report to U.S. Army Engineer District, Honolulu, 70 p.

The importance of holocentrids as predators has been well documented (Randall, 1967; Hobson, 1974; Vivien and Peyrot-Clausade, 1974; Gladfelter and Johnson, 1983). Gladfelter and Johnson (1983) found that seven species of squirrelfishes made up >99% of the nocturnally active, benthic crustacean-feeding fishes at St. Croix, U.S. Virgin Islands. Randall (1967) reported that holocentrids accounted for about 14% by number and 11% by weight of all zooplankton consumed as prey by the fish community at St. John, U.S. Virgin Islands. In the NWHI, holocentrids, including *M. amaena*, are among the most successful families of fish predators. Holocentrids accounted for nearly 40% by number, over 60% by weight, and about 50% by volume of the large crustacean community (crabs, shrimps, stomatopods, and lobsters) taken as prey by the 78 fish species from 28 families that contained large crustacean prey in our NWHI diet studies. Holocentrids also were responsible for about 2.5% of all the individual fish eaten. The fraction of the complete food consumption (all prey in the community combined) by this entire fish community that is eaten by holocentrids was about 13–17% (Parrish, unpubl. data).

Holocentrids also are an important element of the community as prey for other fishes. In the NWHI, 4% of all identified fish prey individuals were holocentrids (Norris and Parrish, 1988). In the western Atlantic, Randall (1967) found evidence that seven species of fishes from four families had eaten holocentrids; three species from three families had eaten Myripristinae (*Myripristis jacobus*). Dragovich (1970) also found that postlarval holocentrids (including Myripristinae) were fairly common prey of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, in the western Atlantic. As a widespread and abundant group that is an active predator and vulnerable prey, holocentrids play a major role in the trophic structure of tropical marine ecosystems.

Reproduction

For specimens from JA, the results from the three independent analyses of gonads (histology, GSI, and visual examination) indicated that sexual maturity of *M. amaena* occurs at 153–156 mm SL for females and at 149–156 mm SL for males. These results correspond closely to SFR estimates from our specimens collected at Puako: 145–160 mm SL, sexes combined (Hayes et al., 1982). Data from both locations are included in Figures 1 and 2. These values of SFR correspond to about 75–80% of L_∞ (as determined by fitting data from length measurements and otolith increment counts to a von Bertalanffy growth model) and to an age of about six years (Fig. 8 in Dee and Radtke, 1989). Dee and Radtke (1989) aged specimens up to nearly 14 years old. Their oldest specimen (of many available for analysis) was somewhat larger than the L_∞ derived from the regression, so it seems unlikely that many individuals live much longer. Therefore, the age at first reproduction (AFR) is probably about 40% (or a little less) of the maximum lifespan commonly attained, and some individuals may reproduce for as many as eight years.

The relation between SFR and maximum body size has been investigated by several workers in a number of locations. The only results reported for squirrelfishes are estimates, based on large sample sizes, for two species of Holocentrinae from the Caribbean Sea (Wyatt, 1976). For *Holocentrus adscensionis*, FL at sexual maturity was about 175 mm, asymptotic (maximum) FL about 265 mm, and the ratio about 0.66; for *Holocentrus rufus*, FL at sexual maturity was about 130–135 mm, asymptotic FL about 230 mm, and the ratio about 0.59. Both these species reach considerably larger sizes than *M. amaena*, and *M. amaena* has the largest SFR/L_∞ ratio of the three species. The ratios for these squirrelfishes seem to be in the high portion of the range of published values for tropical fishes (Munro, 1974; Loubens, 1980). *Myripristis amaena*, in particular, matures at an advanced absolute age and at a surprisingly large fraction of its maximum age and size.

Spawning of *M. amaena* at JA seems to occur primarily in April–May; a secondary peak probably takes place in late September. All specimens collected during the fall peak showed GSI values above the inactive (off-season) level, but considerably below the mean value for the spring peak (Fig. 5). Although no collections were possible in September, visual examination and GSI data from collections made throughout October 1985 suggested the late stages of a spawning period that probably peaked in late September. Back calculation using the total number of otolith increments counted for the two smallest individuals aged by scanning electron microscope examination (Dee and Radtke, 1989) indicated that one individual was spawned in late September and the other in early October. A spawning peak also was observed in specimens collected in January 1986, but not in January 1985. The 1986 event may have resulted from unseasonably calm conditions that occurred during that period. Spawning also was recorded during January 1986 for *Chaetodon trifascialis*, an unusual time of year for that species. Values of the GSI for *M. amaena* collected in January 1986 were generally as high as those of specimens collected during the April spawning peak.

Data were not collected at Puako in a way that would permit a comparable assessment of seasonal

distribution of reproduction. Instead, small collections of specimens were made at regular, frequent intervals only long enough to discern a time of active reproduction. At only that time, a large collection of specimens was made quickly to permit estimation of SFR, and seasonal collections were not continued (Hayes et al., 1982). Thus, the Puako results serve only to establish that reproductive development (e.g. GSI, Fig. 5) is high in May and June. Those months probably represent a peak, but the data do not well define its limits or the pattern for the rest of the year. This early summer high at Puako is contiguous with the late spring high at JA.

Many tropical marine species show a collective spring spawning peak and a second peak in fall (Munro et al., 1973; Watson and Leis, 1974; Johannes, 1978; Walsh, 1987). For Hawaiian fishes, the most dominant seasonal spawning pattern, based on numbers of spawning records, is a peak spawning period in about April and May, with a secondary peak in October for some species. Based on numbers of recruitment records, the dominant recruitment period occurs in June and July, and a secondary peak in February and March (Walsh, 1987). Many studies indicate that there can be considerable variability in the timing of recruitment from year to year, and that the timing and intensity may vary at small spatial scales (Victor, 1982; Williams, 1983; Sale, 1985; Schroeder, 1985; Walsh, 1987, Doherty, 1991).

Larval and newly settled *M. amaena* were elusive throughout the present study, and few data could be collected regarding recruitment. The youngest specimen for which we counted short period (apparently daily) increments in otoliths (Dee and Radtke, 1989) showed a discontinuity that probably represented settlement from the plankton. Back calculation based on the number of increments after the assumed settlement mark suggests that the specimen settled in early February. Although our data regarding settlement are minimal, both these and our spawning results are consistent with the above seasonal reproductive periods summarized by Walsh (1987). Walsh suggested that changes in water temperature or photoperiod, or both, are most likely responsible for observed seasonal patterns of spawning and recruitment in Hawaiian reef fishes. For *M. amaena* at JA, there was no indication that water temperature affected the time of spawning. The full annual range of temperature is very small (24.5–26.5°C). Temperatures during the reproductive period of January 1986 were among the coldest recorded during the entire study, whereas temperatures during spawning in April 1984 were among the highest recorded.

Wyatt (1976) reported on spawning seasons of two Holocentrinae species in Jamaican waters. He recorded ripe *Holocentrus adscensionis* collected in all months except June, and only 2% (one specimen) ripe in July. Most spawning occurred in January, February, and March, but October was also a peak month. Besides ripe fish, "sexually active" gonads were common (14–37% of all gonads) in September through May. The seasonal pattern was similar for *H. rufus*; highest peaks of ripe gonads occurred in October (44%) and February (32%). "Sexually active" gonads were found in all months except July. May, June, and July were the months of lowest gonad development. In Bermuda (15° farther north in mid-ocean), Winn et al. (1964) reported breeding by both these Holocentrinae species in June, July, and August. Variability in timing of spawning due to factors such as lunar periodicity, water temperature, plankton productivity, photoperiod, currents, and rainfall occurs commonly, and spawning time can vary from year to year, even at the same location (Watson and Leis, 1974; Wyrtki, 1974; Johannes, 1978; Walsh, 1987).

The fecundity of *M. amaena* is relatively low compared with many marine species. The most fecund specimen examined contained fewer than 70,000 maturation stage eggs, and the length-fecundity function predicts that a specimen of length L_∞ would contain fewer than 100,000 such eggs. Fecundity increases sharply with body size; it rises with the fifth power of weight and more than the tenth power of SL. (The sample size used for the regressions was not large, but the values of r^2 indicate a reasonably good fit.) These changes with size are much greater than those found in many marine species. These results, together with the results for SFR and the oldest specimen aged, indicate that the species matures slowly. With a relatively long life and steeply increasing fecundity, a very large fraction of the reproductive output of the population is provided by old fish.

The number of spawnings per year is unknown. There was no clear evidence in ovaries examined under direct light microscopy or histologically of a distinct series of distinguishable groups of ova in a graded-size sequence that might represent serial batches spawned within a season. However, production of such serial clutches is commonplace in tropical, nearshore fishes. Unless individual females spawn a good many batches (of the full number of maturation stage eggs estimated) within each year, the total or lifetime fecundity of individuals is relatively low compared with many common marine species. For example, an individual maturing at age six and spawning once annually through age 14, according to the body sizes indicated by our von Bertalanffy expression (Dee and Radtke, 1989) and the fecundity indicated by our length-fecundity expression, would produce fewer than 300,000 eggs during such

a reproductive life. Clearly, determination of the number of clutches spawned in a reproductive season is an important subject for research on *M. amaena*.

Most types of fisheries tend to produce higher mortality of older age classes. Certainly this is true of the common spear fisheries for squirrelfish in the tropics, where larger specimens are individually selected. For a species in which sexual maturity and fecundity are related to age (size) as they are in *M. amaena*, this means that substantial fishing pressure applied to the population can severely reduce egg production (see Fig. 7). The risks of recruitment overfishing are therefore especially great, particularly when maturity occurs late enough that fish of prereproductive size are still a desirable catch. The expected trend as fishing pressure on such a stock increases is the appearance of an increasing fraction of prereproductive fish in the catch. At JA, despite low total fishing effort, about 51% of all *M. amaena* in our creel sample of the fishery were prereproductive; in the small-scale, recreational-subsistence fishery at Puako, about 46% were prereproductive (n=24). Near many centers of human population, fishing intensity is much greater, and great declines in populations of soldierfish are unofficially reported. Clearly the life history of *M. amaena*, and perhaps soldierfishes in general, creates high vulnerability to conventional, unregulated fishing. It seems essential that fisheries for such species be managed to conserve the largest, oldest spawners to protect the reproductive potential of the stock.

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Literature cited

Alldredge, A. L., and J. M. King.
1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar. Biol. (Berl.) 41:317–333.

Amerson, A. B., and P. C. Shelton.
1976. The natural history of Johnston Atoll, central Pacific Ocean. Atoll Res. Bull. 192:1–479.

Brecknock, E. L.
1969. Some aspects of the ecology of *Myripristis murdjan* in the Hawaiian Islands. M.S. thesis, Univ. Hawaii, Honolulu, 22 p.

Dee, A. J., and R. L. Radtke.
1989. Age and growth of the brick soldierfish, *Myripristis amaena*. Coral Reefs 8:79–85.

Doherty, P. J.
1991. Spatial and temporal patterns in recruitment. *In* P. F. Sale (ed.), The ecology of fishes on coral reefs. Academic Press, San Diego, 754 p.

Dragovich, A.
1970. The food of the skipjack and yellowfin tunas in the Atlantic Ocean. U.S. Fish Wildl. Serv., Fish. Bull. 68:445–460.

Gladfelter, W. B., and W. S. Johnson.
1983. Feeding niche separation in a guild of tropical reef fishes (Holocentridae). Ecology 64:552–563.

Greenfield, D. W.
1965. Systematics and zoogeography of *Myripristis* in the eastern tropical Pacific. Calif. Fish Game 51:229–247.
1968. The zoogeography of *Myripristis* (Pisces: Holocentridae). Syst. Zool. 17:76–87.

1974. A revision of the squirrelfish genus *Myripristis* Cuvier (Pisces: Holocentridae). Los Angel. Cty. Mus. Sci. Bull. 19:1–54.

Guyer, M. F.
1953. Animal micrology, 5th ed. Univ. Chicago, 327 p.

Halstead, B. W., and N. C. Bunker.
1954. A survey of the poisonous fishes of Johnston Island. Zoologica (N.Y.) 39:61–77.

Harmelin-Vivien, M. L.
1979. Ichtyofaune des recifs coralliens de Tulear (Madagascar): ecologie et relations trophiques. Annexe D.Sc. these, Univ. Aix-Marseille II, 116 p. [In French.]
1981. Trophic relationships of reef fishes in Tulear (Madagascar). Oceanol. Acta 4:365–374.

Hayes, T. A., T. F. Hourigan, S. C. Jazwinski Jr., S. R. Johnson, J. D. Parrish, and D. J. Walsh.
1982. The coastal resources, fisheries and fishery ecology of Puako, West Hawaii. Hawaii Cooperative Fishery Research Unit Tech. Rep. 82-1, 159 p.

Hiatt, R. W., and D. W. Strasburg.
1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30:65–127.

Hobson, E. S.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull. 70:715–740.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull. 72:915–1031.

Humason, G. L.
1979. Animal tissue techniques, 4th ed. Freeman, San Francisco, 661 p.

Johannes, R. E.
1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fishes 3:65–84.

Khoo, H. K.
1978. The histochemistry and endocrine control of vitellogenesis in goldfish ovaries. Can. J. Zool. 57:617–626.

Loubens, G.
1980. Biologie de quelques espèces de Poissons du lagon neo-caledonien. II: Sexualite et reproduction. Cahiers de l'Indo-pacifique 2(1):41–72. [In French.]

Maragos, J. E., and P. L. Jokiel.
1986. Reef corals of Johnston Atoll: one of the world's most isolated reefs. Coral Reefs 4:141–150.

Munro, J. L.
1974. The biology, ecology, exploitation and management of Caribbean reef fishes. Part V.m: Summary of biological and ecological data pertaining to Caribbean reef fishes. ODA/UWI Fisheries Ecology Research Project: 1969–1973. Research report from the Zoology Dept., Univ. West Indies. No. 3. Kingston, Jamaica, 24 p.

Munro, J. L., V. C. Gaut, R. Thompson, and P. H. Reeson.
1973. The spawning seasons of Caribbean reef fishes. J. Fish Biol. 5:69–84.

Norris, J. E., and J. D. Parrish.
1988. Predator-prey relationships among fishes in pristine coral reef communities. *In* J. H. Choat et al. (eds.), Proc. sixth int. coral reef symposium, Townsville, Australia, 8–12 Aug. 1988, vol. 2, p.107–113. Sixth Int. Coral Reef Symp. Exec. Comm.

Oda, D. K., and J. D. Parrish.
1982. Ecology of commercial snappers and groupers introduced to Hawaiian reefs. *In* E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh Jr., and R. T. Tsuda (eds.), Proc. fourth int. coral reef symposium, Manila, 18–22 May 1981, vol. 1, p. 59–67. Marine Sciences Center, Univ. Philippines, Quezon City, Philippines.

Parrish, J. D.
1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions. Mar. Ecol. Prog. Ser. 58:143–160.

Parrish, J. D., M. W. Callahan, and J. E. Norris.
1985. Fish trophic relationships that structure reef communities. *In* C. Gabrie and B. Salvat (eds.), Proc. fifth int. coral reef congress, Tahiti, 27 May–1 June 1985, vol. 4, p. 73–78. Antenne Museum-EPHE, Moorea, French Polynesia.

Pinkas, L., M. S. Oliphant, and I. Iverson.
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. Calif. Dep. Fish Game, Fish Bull. 152:1–105.

Porter, J. W., and K. G. Porter.
1977. Quantitative sampling of demersal plankton migrating from different coral reef substrates. Limnol. Oceanogr. 22: 553–556.

Randall, J. E.
1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665–847.

Randall, J. E., and P. Gueze.
1981. The holocentrid fishes of the genus *Myripristis* of the Red Sea, with clarification of the *murdjan* and *hexagonus* complexes. Los Angel. Cty. Mus. Contrib. Sci. 334, 16 p.

Randall, J. E., P. S. Lobel, and E. H. Chave.
1985. Annotated checklist of the fishes of Johnston Island. Pac. Sci. 39:24–80.

Sale, P. F.
1985. Patterns of recruitment in coral reef fishes. *In* C. Gabrie and B. Salvat (eds.), Proc. fifth int. coral reef congress, Tahiti, 27 May–1 June 1985, vol. 5, p. 391–396. Antenne Museum-EPHE, Moorea, French Polynesia.

Schroeder, R. E.
1985. Recruitment rate patterns of coral reef fishes at Midway lagoon, Northwestern Hawaiian Islands. *In* C. Gabrie and B. Salvat (eds.), Proc. fifth int. coral reef congress, Tahiti, 27 May–1 June 1985, vol. 5, p. 379–384. Antenne Museum-EPHE, Moorea, French Polynesia.

ter Kuile, C.
1989. The forage base of some reef fishes in the Flores Sea with notes on sampling and fishery. Neth. J. Sea Res. 23:171–179.

Victor, B. C.
1982. Daily otolith increments and recruitment in two coral-reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. Mar. Biol. (Berl.) 71:203–208.

Vivien, M. L., and M. Peyrot-Clausade.
1974. A comparative study of the feeding behaviour of three coral reef fishes (Holocentridae), with special reference to the polychaetes of the reef cryptofauna as prey. *In* A. M. Cameron, B. M. Campbell, A. B. Cribb, R. Endean, J. S. Jell, O. A. Jones, P. Mather, and F. H. Talbot (eds.), Proc. second int. symp. coral reefs, Great Barrier Reef Province, Australia, 22 June–2 July 1973, vol. 1, p. 179–192. The Great Barrier Reef Committee, Brisbane.

Wallace, R. A., and K. Selman.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

Walsh, W. J.
1987. Patterns of recruitment and spawning in Hawaiian reef fishes. Environ. Biol. Fishes 18:257–276.

Watson, W., and J. M. Leis.
1974. Ichthyoplankton in Kaneohe Bay, Hawaii. A one year study of fish eggs and larvae. Univ. Hawaii Sea Grant Technical Report TR–75–01, 178 p.

Williams, D. M.
1983. Daily, monthly and yearly variation in recruitment of juvenile coral reef fishes to coral habitats within One Tree Lagoon, Great Barrier Reef. Mar. Biol. (Berl.) 65:245–253.

Winn, H. E., J. A. Marshall, and B. Hazlett.
1964. Behavior, diel activities, and stimuli that elicit sound production and reactions to sounds in the longspine squirrelfish. Copeia 1964:413–425.

Wolfert, D. R., and T. J. Miller.
1978. Age, growth, and food of northern pike in eastern Lake Ontario. Trans. Am. Fish. Soc. 107:696–702.

Wyatt, J. R.
1976. The biology, ecology, exploitation and management of Caribbean reef fishes. Va: The biology, ecology and bionomics of Caribbean reef fishes: Holocentridae (squirrelfishes). ODA/UWI Fisheries Ecology Research Project: 1969–1973. Research report from the Zoology Dep., Univ. West Indies. No. 3. Kingston, Jamaica. 41 p.

Wyrtki, K.
1974. Sea level and seasonal fluctuations of the equatorial currents in the western Pacific Ocean. J. Physical Oceanogr. 4:91–103.

Appendix A

Relationships between standard length (SL), fork length (FL), and total length (TL) in millimeters, based on linear regressions for 377 specimens of the brick soldierfish, *Myripristis amaena*, from Johnston Atoll (JA).

$$SL = 0.9013\ FL - 3.22, \quad r^2 = 0.991$$
$$SL = 0.7811\ TL - 3.23, \quad r^2 = 0.992$$
$$TL = 1.1493\ FL + 0.65, \quad r^2 = 0.991$$

Appendix B

Size measured and batch fecundity estimated by counting ova in aliquots from the ovaries of 12 specimens of the brick soldierfish, *Myripristis amaena*, from Johnston Atoll (JA).

Standard body length (mm)	Whole body wet weight (g)	Estimated batch fecundity
156	149	12402
166	162	12925
168	167	17077
169	166	17618
175	189	29505
175	187	57200
177	191	47680
179	190	42003
180	189	25301
181	225	69221
187	209	61000
188	211	66719

Reproductive biology of the cockfish, *Callorhynchus callorhynchus* (Holocephali: Callorhynchidae), in Patagonian waters (Argentina)

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Abstract.—*Callorhynchus callorhynchus* Linnaeus ("cockfish" or "pez gallo"), the only holocephalan fish species found in the coastal waters of the southwestern Atlantic Ocean, has been caught off Argentina as bycatch of the hake, *Merluccius hubbsi*, fishery since 1920. Here we describe the morphology of its reproductive system and report on several aspects of its reproductive biology. This study is based on survey data and sampling of commercial landings from San Matías Gulf (41–42°S; 64–65°W), conducted from 1984 to 1986.

The data suggest that reproductive activities extend nearly throughout the year; mating and spawning occur in spring and early summer, followed by a short period (ca. one month) of gonadal recovery. Average size at sexual maturity (standard length, measured from the tip of the mouth to the origin of the superior caudal lobe) is 40 cm for males and 49 cm for females. Male gonadal and green gland indices peak asynchronously. During the mating season the green gland forms spermatophores that are transferred to the female at the time of copulation. The cloaca of adult females has a seminal receptacle where the mass of spermatophores is stored after copulation. Female gonadal and nidamental gland indices peak synchronously. After fertilization the oocytes are encapsulated before spawning. Oocyte diameter increases with the size of females up to a maximum of 48 mm.

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The cockfish, *Callorhynchus callorhynchus* Linnaeus, 1758, is the only holocephalan fish species found in the coastal waters of the southwestern Atlantic Ocean (Norman, 1937; Hart, 1946; Menni and Gostonyi, 1982). Adults are caught as bycatch of the hake, *Merluccius hubbsi*, fishery that operates off Argentina (Di Giácomo and Perier, 1991). Although there is considerable concern with regard to harvesting fish species with comparatively low reproductive potential (such as many elasmobranch and holocephalan species), the reproductive biology and life history of the cockfish are poorly known. In this study we describe the morphology of the reproductive system of *C. callorhynchus* and present information on its reproductive biology.

Materials and methods

Bottom trawl surveys

A survey off the north coast of San Matías Gulf (northern Patagonia; 41–42°S, 64–65°W; Fig. 1) was conducted from 15 to 19 October, 1986, aboard the FRV *C. Cánepa*. Thirty three 30-minute hauls were made at depths ranging from 20 m to 130 m, by using a 96-foot commercial otter trawl with rectangular doors (Di Giácomo and Perier, 1991). All specimens of *C. callorhynchus* were processed following laboratory procedures described below.

Sampling of the commercial landings

The commercial catch of the bottom trawl fishery landed in San Antonio Oeste (40°43'04"S, 64°56'W) was sampled monthly between February 1984 and July 1986. On each sampling date three boxes (N=20 fish per box) weighing 37 kg each were randomly selected. Samples of the commercial catch were not available during April, September, June, and December because either the fishery was inactive or no cockfish were landed.

Laboratory procedures

Standard length (SL, distance from the tip of the snout to the origin of the upper caudal lobe, Fig. 2A), total weight and liver weight were obtained from each fish sampled. Specimens were dissected to expose the reproductive system; testes and green glands of males, and ovaries and nidamental glands of females were individually weighed. The number of mature yolk oocytes and immature oocytes, maximum diam-

eter of the oocytes, number of individuals with egg cases in formation or ready for extrusion, and presence of spermatophores were recorded for females. Length of the myxopterygia (males) was measured from the insertion of the pelvic fin to the distal end (Fig. 2B).

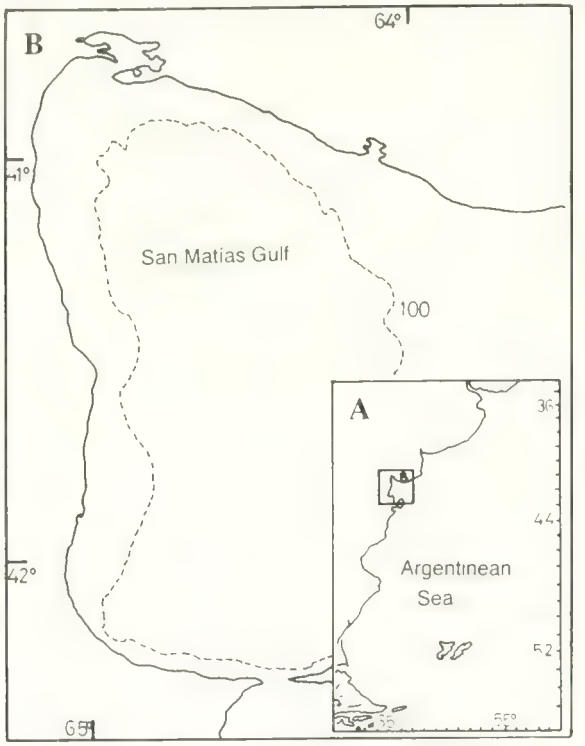

Figure 1

(**A**) Location of the study area in the Argentinean continental shelf; (**B**) San Matías Gulf.

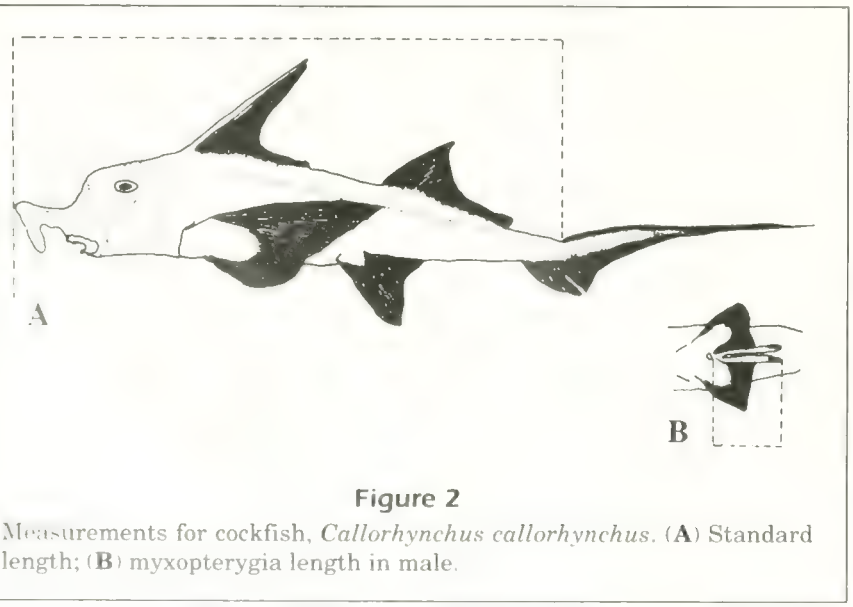

Figure 2

Measurements for cockfish, *Callorhynchus callorhynchus*. (**A**) Standard length; (**B**) myxopterygia length in male.

Indices of reproductive activity

The annual reproductive cycle was assessed by using the monthly samples of the commercial catch (1984–86). The gonadal index (GI), hepatic index (HI), nidamental gland index (NGI, females only) and green gland index (GGI, males only) were calculated as

$$GI = \frac{\text{weight of the gonad}}{\text{total weight}} \times 100$$

$$HI = \frac{\text{weight of the liver}}{\text{total weight}} \times 100$$

$$NGI = \frac{\text{weight of the nidamental gland}}{\text{total weight}} \times 100$$

$$GGI = \frac{\text{weight of the green gland}}{\text{total weight}} \times 100.$$

The duration of the mating season was estimated from the presence of spermatophore masses in the female cloaca and the annual cycle of the green gland index.

Regression analysis was performed between the indices of reproductive activity during the periods of maximum activity and SL, and between the diameter of mature oocytes and the number of immature oocytes and SL. A Wilcoxon test was used to assess the difference in the average number of mature ova between right and left ovaries of all mature females.

Sexual maturity

The degree of development of the myxopterygia (male claspers) relative to SL was used as an indicator of sexual maturity for males (Holden and Raitt, 1975). The size at first maturity in females was determined by examining 1) the percentage of mature females in each 10-mm size class, 2) the maximum diameter of mature ovarian eggs for each size class, and 3) the smallest size class with egg cases in formation. Females with yellow ovarian eggs were considered mature.

Results

Morphology of the reproductive system

The male reproductive system consists of the following paired struc-

tures: testes, epididymis (efferent ducts), and deferent ducts (Leigh-Sharpe, 1922). In sexually mature individuals, the deferent ducts are differentiated into two fusiform structures called green glands (Fig. 3A). These structures agglutinate the spermatozoa into spermatophores and secrete a gelatinous, green fluid. The reproductive system of the female is composed of the following paired structures: ovaries, oviducts, nidamental or shell glands, uteri, and vaginal openings that end in a cloaca (Fig. 3B).

Holocephalans are sexually dimorphic. Male secondary sexual structures (frontal tenaculum, and prepelvic and pelvic claspers) are utilized during mating (Fig. 4); the male apparently inserts the mass of spermatophores into the seminal receptacle of the female cloaca. Upon macroscopic examination (October), a mass of spermatophores was found at the female genital opening. Spermatozoa are liberated progressively by an unknown mechanism, before fertilization.

Females extrude fertilized eggs enclosed within a leathery case (Dean, 1906) that acts as protection for the embryo during development. At hatching the fry resembles the adult.

Indices of reproductive activity

The GI of males reached a maximum in March (3.0) and was low from July to October (range seen in Fig. 5A). The highest mean values of the GGI were found between July and October (Fig. 5B), although the index was also high during January and February. In females, the GI reached its highest values from July to October, indicating low reproductive activity during the rest of the year (Fig. 6A). The NGI (females) has two periods of activity: July to November (highest) and January to June (lowest) (Fig. 6B). The HI for both males and females (Fig. 5C, 6C) did not show significant annual fluctuations; maximum values occurred simultaneously with peaks in the other reproductive indices.

Mature and immature females could be differentiated based on GI values (range: 0.13 to 4.55); a GI value larger than 1.0 was characteristic of mature females. The presence in March of some females smaller than 50 cm SL with a GI higher than 1.0 and ovaries with translucent oocytes was suggestive of oocyte resorption. Oocyte diameter varied between 10 and 35 mm.

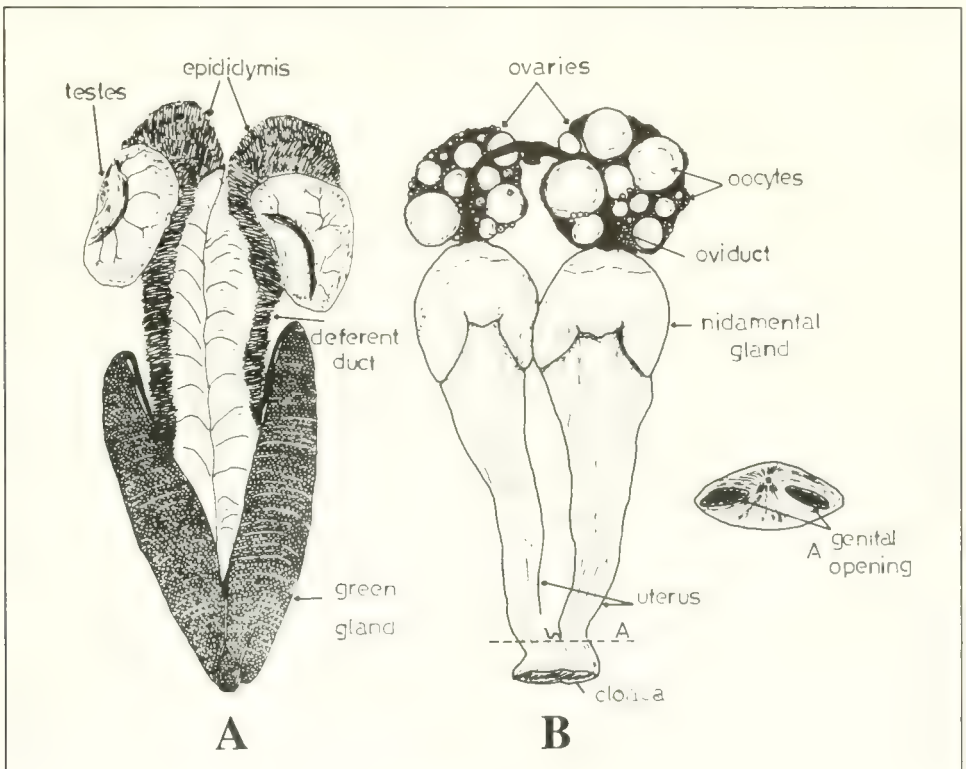

Figure 3

Reproductive organs of the cockfish, *Callorhynchus callorhynchus*. (**A**) Males; (**B**) females.

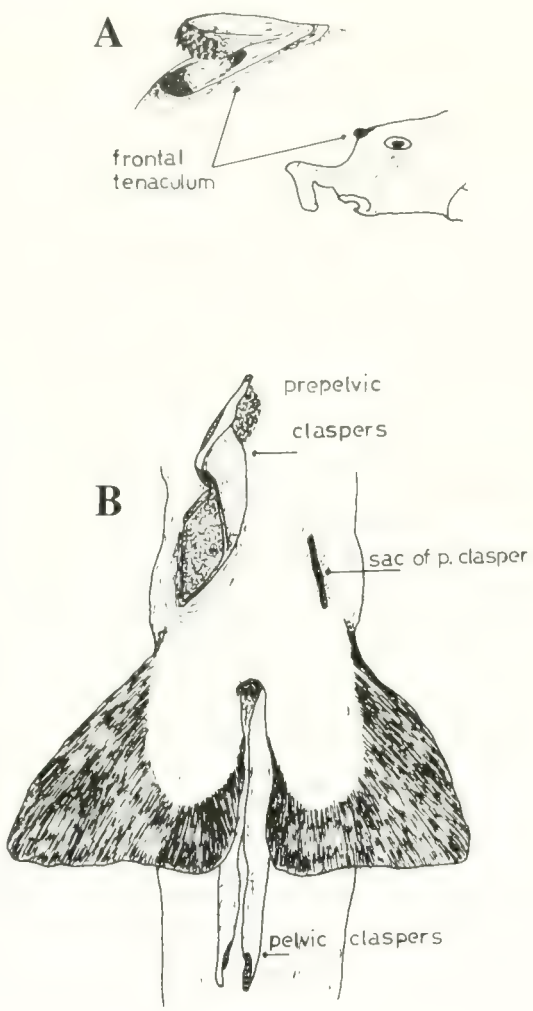

Figure 4

Male secondary sexual structures of cockfish, *Callorhynchus callorhynchus*. (**A**) Frontal tenaculum; (**B**) prepelvic and pelvic claspers.

Gonad and green gland indices were highly variable within size classes during the period of maximum activity. There was no relationship between SL and GI (r^2=0.001; P>0.05; N=121), or between SL and GGI (r^2=0.021; P>0.05; N=101). Similarly, no relationship was found between female SL and GI (r^2=0.18; P>0.05; N=58) or NGI (r^2=0.012; P>0.05; N=48).

Size at sexual maturity

Immature and mature males could be identified from the relationship between SL and length of the myxopterygia. The myxopterygia did not exceed the posterior margin of the pelvic fin in immature individuals, whereas in mature individuals it consisted of partially calcified structures that exceeded the posterior margin of the pelvic fin. The length of fish measured (N=123) ranged from 26 cm to 55 cm. Length at first maturity of males was estimated to be 40 cm, corresponding to a length of the myxopterygia of 45 mm. No individuals between juvenile and mature stages were observed. Juvenile stages were found in shallow waters (depth range 15–25 m) whereas adults were found in waters deeper than 25 m (Di Giácomo, 1992). Most mature females were larger than 50 cm (SL), whereas all females smaller than 48 cm were immature.

Ovarian maturation

The percentage of mature oocytes was greatest in August in both ovaries, coinciding with maxima in the indices of reproductive activity. Nevertheless, some mature oocytes were observed throughout the year (Fig. 7A). Mean number of mature oocytes was highest from July to October. There was a significant difference between the average number of mature oocytes in the right and left ovaries of individual mature females (Wilcoxon test, P<0.05; Fig. 7B).

Oocyte diameter increased with female size (r^2=0.083; P<0.01; N=90). Maximum oocyte diameter (48 mm) was recorded for a female of 71 cm SL. The regression of number of immature oocytes on SL showed a similar trend, indicating that average reproductive potential increases with size (r^2=0.024; P<0.01; N=101).

Oocytes smaller than 10 mm (diameter) were translucent to lightly whitish. Coloration of oocytes larger than 10 mm changed gradually. Yolk was incorporated until the oocytes reached complete development and passed to the nidamental gland. Production of egg cases began in the nidamental gland, when the oocytes reached maturity. The closed end of the egg case was caudally oriented; the cephalic portion remained open until the case was completely formed. When the egg case was about two-thirds of its final size, ovulation occurred and the egg (with a variable diameter that ranged from 40 to 48 mm) moved from the ovaries, through the oviduct, to the case.

Mating season

Spermatophores were found in the vaginal receptacles associated with the female cloaca. Mating occurred primarily from July to February, when maxima in the GGI were indicative of active production of spermatophores. The highest percentage of females with spermatophores in the cloaca was also observed during these months (Fig. 8). In October, recently deposited spermatophores in the female cloaca, characterized macroscopically by an intense green color, resembled green gland products. Yellowish spermatophores found in March and May (when

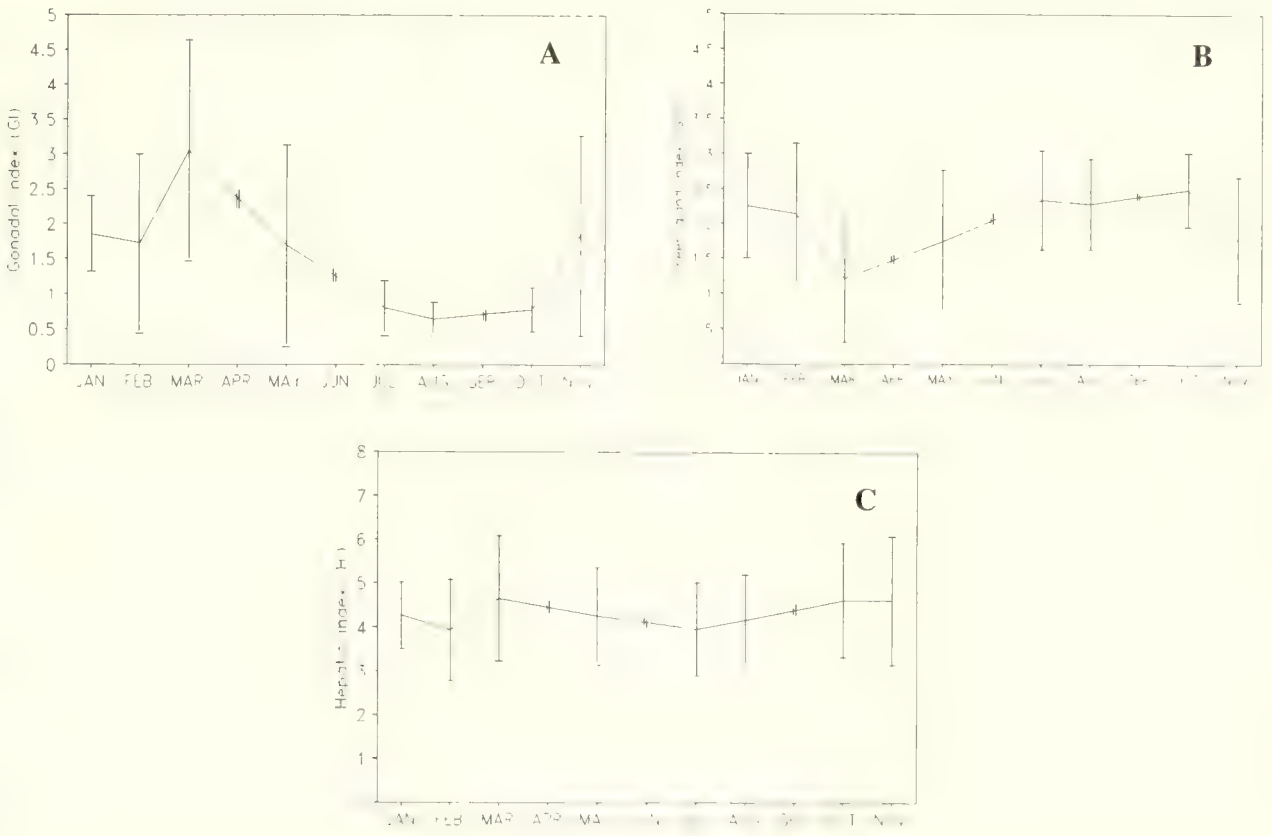

Figure 5

Indices of reproductive activity of males of the cockfish, *Callorhynchus callorhynchus*. (**A**) Gonadal index (GI); (**B**) green gland index (GGI); (**C**) hepatic index (HI).

the green gland index was low) probably remained from copulation during the previous year. After insemination, the spermatophores were apparently mobilized by the female in coordination with the production of egg cases in order to fertilize the oocytes.

Spawning season

The primary spawning season extended from July to November. The mean size of females with egg cases in formation increased from July to November (Fig. 8). Egg cases in an early stage of development were found in bottom trawl catches at 105 m, whereas females with egg cases with embryos almost fully developed were found in bottom dredge catches at depths ranging from 20 to 40 m.

Discussion

Morphology

The morphology of the reproductive system of holocephalan fishes has been described for *Chimaera monstrosa* and *Callorhynchus antarcticus* (Leigh-Sharpe, 1922; Legendre, 1944), and *Hydrolagus colliei* (Cox, 1963). Species of living holocephalans are generally reported to lack a cloaca (Grasse, 1958; Lagler et al., 1977); Malagrino et al. (1981) mentioned the absence of a cloaca in females of *Chimaera phantasma* as characteristic of the group. This contrasts with the elasmobranchs, in which the female genital ducts terminate in the cloaca. Stanley (1963) noted the presence of a cloaca in newly hatched males and females of *H. colliei*, which is lost as they grow. *Callorhynchus callorhynchus*, by contrast, has a cloaca with a seminal receptacle where the spermatophores are stored.

Reproductive cycle

The peak of the male GI indicates the season when testicular activity is at a maximum. The delay between maxima in GGI and GI may reflect a sequence of phenomena: 1) production of spermatozoa in the testes, 2) movement of spermatozoa through the ef-

ferent ducts and the first part of the deferent ducts, and 3) accumulation in the green gland during the formation of spermatophores. Activity of the female gonads and nidamental glands is synchronous because as the oocytes mature they are ovulated and immediately encapsulated in the nidamental glands.

Unlike most elasmobranch species in which one ovary is functional and the other is vestigial (Mellinger, 1972; Menni et al., 1979; Teshima, 1981; Natanson and Cailliet, 1986; Smith and Merriner, 1986), the left and right ovaries of *C. callorhynchus* are both functional. However, the average number of ova produced in each ovary is different. As in *H. colliei*, the egg cases of *C. callorhynchus* are produced simultaneously by both of the nidamental glands (Dean, 1906).

Changes taking place in the development of the gonad and the green gland of males suggest that reproductive activity is continuous, with a period of rest or recovery around March. Relatively high female index values in February can be considered a continuation of the main period of reproductive activity. The sample of females analyzed in January was probably not representative because of their scarcity in commercial landings. Resting or recovery may last one or two months in *C. callorhynchus*, while males and females of *C. monstrosa* and *C. phantasma* have a resting period of six months (Vu Tan Tue, 1972; Malagrino et al., 1981).

Sexual maturity

A threshold value in the GI has been utilized to separate immature and mature females in some teleost species in which oocytic resorption has not been observed. In *C. callorhynchus* such a GI threshold criterion must be coupled with macroscopic observation of the ova in the ovary; in the case of low GI values, presence or absence of atrophied ova is indicative of resting or immature conditions, respectively.

Development of the myxopterygia is diagnostic of male maturity in *C. callorhynchus*, allowing the identification of the length at first maturity. Transition between stages can be related to an offshore migra-

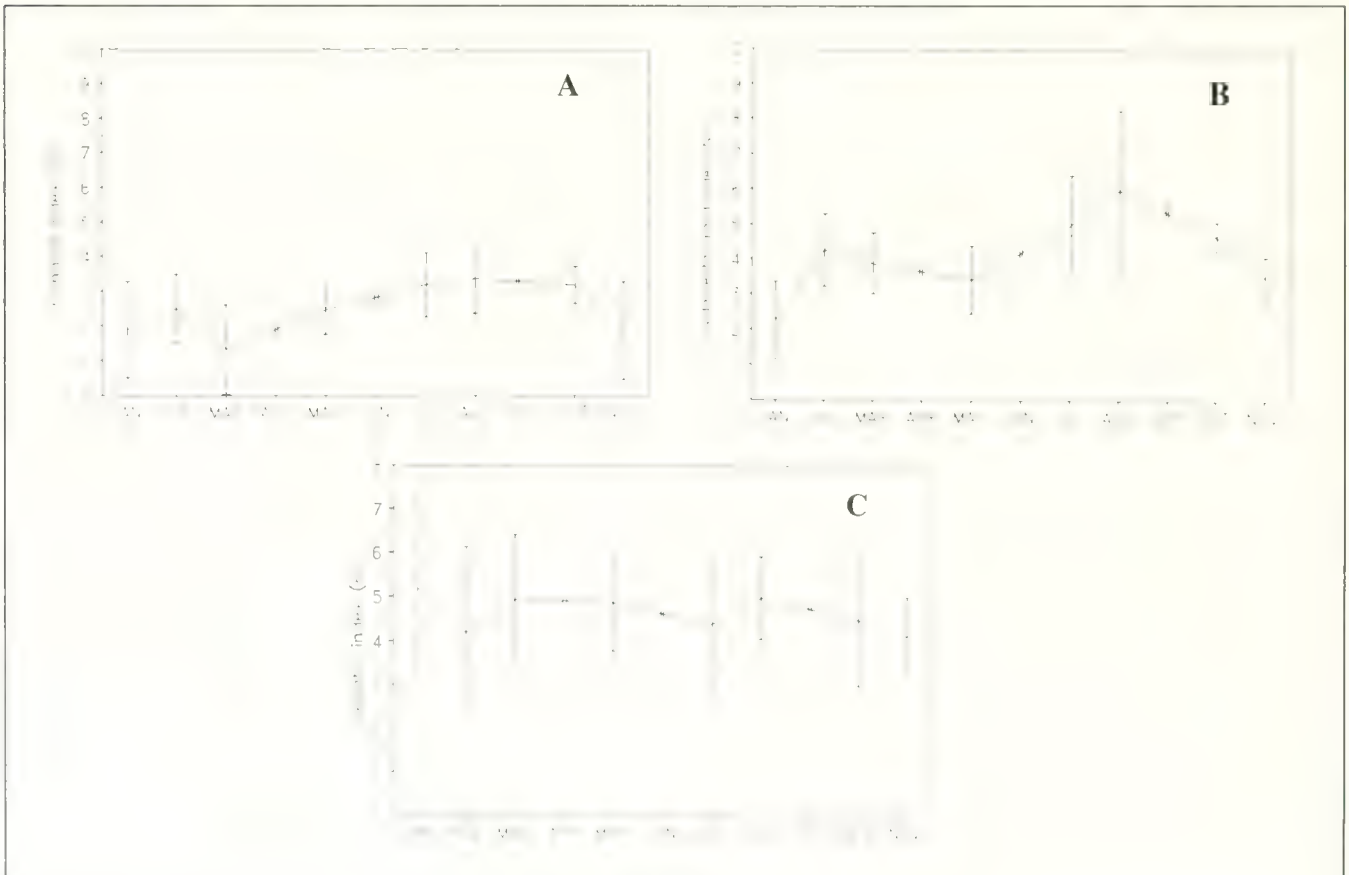

Figure 6

Indices of reproductive activity of females of the cockfish, *Callorhynchus callorhynchus*. (**A**) Gonadal index (GI); (**B**) nidamental gland index (NGI); (**C**) hepatic index (HI).

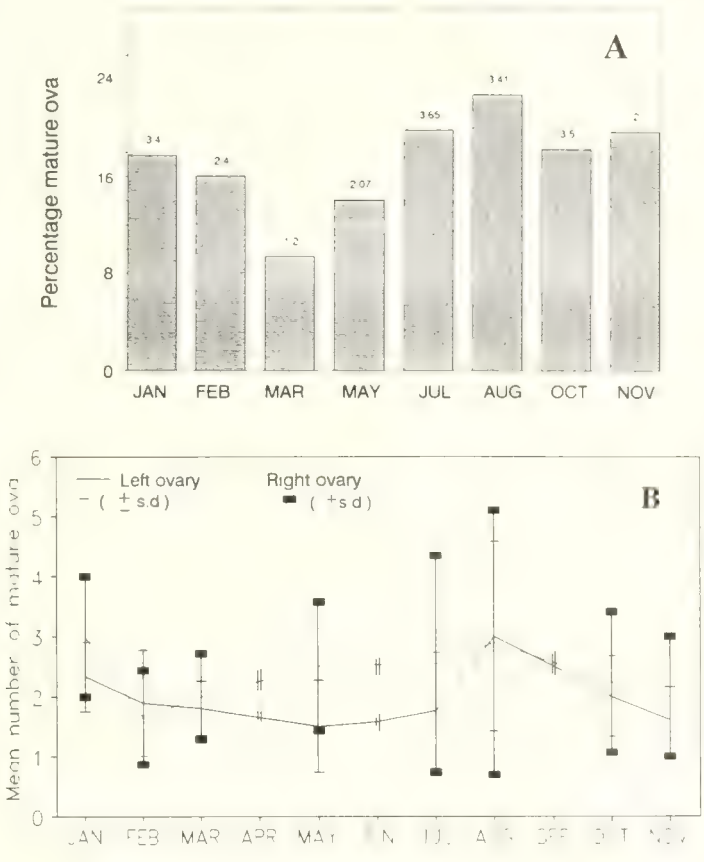

Figure 7

Females of the cockfish, *Callorhynchus callorhynchus*. (**A**) Percentage and average number (numbers above bars) of mature ova by month; (**B**) mean number of mature ova per ovary by month.

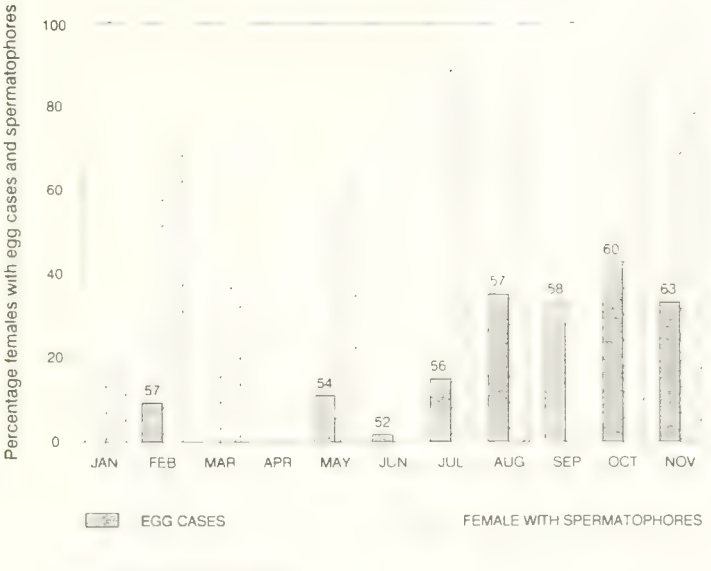

Figure 8

Percentage of spermatophores and developing egg cases in females of the cockfish, *Callorhynchus callorhynchus*, by month.

tion. The absence of intermediate stages in our materials can be explained by the fact that sampling was conducted mostly between 90 and 130 meters, where adults prevail (Di Giácomo, 1992).

Mature females cannot be clearly defined. Holden (1975) defined mature females of the ray *Raja clavata* as those individuals that had large, yellow oocytes in the ovaries. Smith and Merriner (1986) distinguished three stages of sexual maturity in females of the cownose ray, *Rhinoptera bonasus*: immature, maturing, and mature. The mature stage was characterized by the presence of large, yellow oocytes greater than one cm in diameter in the ovaries. The authors accounted for the minimum length of gravid females observed (*R. bonasus* is viviparous). We could not identify which oocytes were ready to be spawned in *C. callorhynchus*. Although all yellow oocytes were viable, resorption may lead to false conclusions regarding spawning state. Therefore, the minimum size fish that had egg cases in formation in the nidamental gland was considered diagnostic, since at that stage resorption is no longer possible. The smallest female with egg cases in formation measured 50 cm (SL), and the smallest female with mature oocytes was 48 cm SL. In females size at first maturity was coincident with the minimum size of fish showing yolked oocytes and egg cases in formation.

McEachran (1970) found that in females of the ray *Raja garmani* the oocytes in the ovaries were half the size of those found in the egg cases. In *C. callorhynchus*, the difference between the maximum size attained by the oocytes in the ovaries and the eggs in the case was about 25%. Assuming a similar speed of yolk incorporation into the oocytes for both species, we estimate that the females of *C. callorhynchus* may have a higher spawning rate than the ray, indicating that maturing oocytes may attain ovulation size faster. The maximum size of mature ova was larger in *C. callorhynchus* than in other holocephalan species such as *Chimaera phantasma* (Malagrino et al., 1981), *C. monstrosa*

(Legendre, 1944), *Hydrolagus colliei* (Dean, 1906), and *Callorhynchus milii* (Gorman, 1963).

Spermatophores

The presence of a "seminal plug" has been reported in *C. milii* (Norman, 1937). Males of *C. monstrosa* form an emerald green substance in the terminal portion of the deferent ducts, but seminal plugs in females have not been reported (Legendre, 1944). There is no seminal plug in *H. colliei*, in which copulation occurs just before eggs are laid (Dean, 1906).

On the basis of our examination of *C. callorhynchus*, we suggest that the term "plug" is improper. It is a seminal mass located in the female's seminal receptacle that does not obstruct the genital ducts and remains in the receptacle during the entire reproductive cycle. The coloration of the spermatophores in the cloaca changes progressively from an intense green to yellow as the spermatophores are mobilized.

Spawning ground

Although we demonstrated seasonality in the mating activity of *C. callorhynchus*, it was not possible to establish where spawning takes place. Quinn et al. (1980) suggested that adults of *H. colliei* migrate to shallow waters during the night. Eighty-five egg cases of *H. colliei* were found at a depth of 11 m, but one capsule was found at 120 m (Dean, 1906). *Callorhynchus monstrosa* spawns at about 100 m (Legendre, 1944); based on its bathymetric distribution (100 to 1700 m), it can be assumed that this species also migrates to the relatively shallow areas to spawn. Females of *C. milii* lay eggs between the surf zone and 37 m, in sand or mud substrata, and move to deeper water after spawning (Gorman, 1963).

Callorhynchus callorhynchus was caught at depths shallower than 170 m in the San Matías Gulf (Di Giácomo, 1992). Egg cases were found between 20–40 m and at 104 m, suggesting that this species may also migrate to shallow water to spawn. Further studies are required to document more conclusively the spawning behavior of females.

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Literature cited

Cox, K. W.
1963. Egg-cases of some elasmobranchs and a cyclostome from Californian waters. Calif. Fish Game 49:271–289.

Dean, B.
1906. Chimaeroid fishes and their development. Publ. Carnegie Inst., Washington, 32, 195 p.

Di Giácomo, E. E.
1992. Distribución de la población del pez gallo (*Callorhynchus callorhynchus*) en el golfo San Matías, Argentina. Frente Maritimo 12(A):113–118.

Di Giácomo, E. E., and M. R. Perier.
1991. Evaluación de la biomasa y explotación comercial del pez gallo (*Callorhynchus callorhynchus*) en el Golfo San Matías, Argentina. Frente Maritimo 9(A):7–13.

Gorman, T. B. S.
1963. Biological and economic aspects of the elephant fish, *Callorhynchus milii* Bory, in Pegasus Bay and the Canterbury Bight. New Zealand Marine Dep. Fisheries Tech Rep. 8, 53 p.

Grasse, P. P.
1958. Super-ordre des holocephali: anatomie, ichtyologie, systematique. *In* Pierre-P. Grasse (ed.), Traite de zoologie; anatomie, systematique, biologie, Vol. 13, Agnathes et poissons, p. 2060–2067. Masson et Cie, Paris.

Hart, J.
1946. Report on trawling surveys on the Patagonian Shelf. Discovery Rep. 23.

Holden, M. J.
1975. The fecundity of *Raja clavata* in British waters. J. Cons. int. Explor. Mer 36:110–118.

Holden, M. J., and D. F. S. Raitt (eds.).
1975. Manual de Ciencia pesquera. Parte 2: Métodos para investigar los recursos y su aplicación. Doc. Téc. FAO Pesca 115 (Rev. 1), 211 p.

Lagler, K. F., J. E. Bardach, R. R. Miller, and D. R. May Passino.
1977. Ichthyology (2nd. ed.). John Wiley & Sons, 506 p.

Legendre, R.
1944. Notes biologiques sur *Chimaera monstrosa* L. Bull. Soc. Zool. France 69:10–17.

Leigh-Sharpe, W. H.
1922. The comparative morphology of the secondary sexual characters of Holocephali and elasmobranch fishes. J. Morphol. 36: 199–243.

Malagrino, G., A. Takemura, and K. Mizue.
1981. Studies on Holocephali. II: On the reproduction of *Chimaera phantasma* Jordan et Snyder caught in the coastal waters of Nagasaki. Bull. Fac. Nagasaki Univ. 51:1–7.

McEachran, C. P.
1970. Egg capsules and reproductive biology of the skate *Raja garmani* (Pisces: Rajidae). Copeia 1970:197–198.

Mellinger, J.
1972. Croissance et reproduction de la torpille (*Torpedo marmorata*). I: Introduction, ecologie, croissance generale et dimorphisme sexuel. Cycle. Fecondite. Bull. St. Biol. Arcachon 24:166–218.

Menni, R. C., and A. E. Gostonyi.
1982. Benthic and semidemersal fish associations in the Argentine Sea. Stud. Neotrop. Fauna Environ. 17:1–29.

Menni, R. C., A. E. Gostonyi, and H. L. López.
1979. Sobre la ecología y biología de *Halaelurus bivius* (Chondrichthyes, Scyliorhinidae). Rev. Museo Arg. Cienc. Nat. (Ecología) 2(3):71–88.

Natanson, L. J., and G. M. Cailliet.
1986. Reproduction and development of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. Copeia 1986:987–994.

Norman, J. R.
1937. Coast fishes. Part II: The Patagonian region. Discovery Rep. 16:35–36.

Quinn, T. P., B. S. Miller, and R. C. Wingert.
1980. Depth distribution and seasonal and diel movements of ratfish, *Hydrolagus colliei*, in Puget Sound, Washington. Fish. Bull. 78:816–821.

Smith, J. W., and J. V. Merriner.
1986. Observations on the reproductive biology of the cownose ray, *Rhynoptera bonasus*, in Chesapeake Bay. Fish. Bull. 84:871–877.

Stanley, H. P.
1963. Urogenital morphology in the chimaeroid fish *Hydrolagus colliei* (Lay and Bennett). J. Morphol. 112:99–128.

Teshima, K.
1981. Studies on the reproduction of Japanese smooth dogfishes *Mustelus manazo* and *M. grisseus*. Bull. Shimonoseki Univ. Fish. 29:115–199.

Vu Tan Tue.
1972. Variations cycliques des gonades et de quelques glandes endocrines chez *Chimaera monstrosa* Linné (Pisces: Holocephali). Ann. Sci. Nat. (Zool.) 12(14):49–94.

The vertical distribution of eggs and larvae of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska*

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Abstract.—The vertical distribution of walleye pollock eggs and larvae in Shelikof Strait, Gulf of Alaska, was investigated by using data from 36 Multiple Opening-Closing Net and Environmental Sensing System (MOCNESS) tows taken in April and May, 1986–88. Most eggs were found below 150 m to near bottom (~300 m) but progressively shallower later in the season. Eggs in middle stages of development were found at shallower depths than were younger or older eggs. The vertical distribution of eggs was positively related to observed differences in seawater temperature but showed no relationship to density. Larvae hatch at incubation depth and quickly rise to the upper 50 m of the water column where they remain during larval development. Larger larvae (~7–10 mm standard length [SL]) undergo limited diel vertical migration within the upper 50 m. They are deepest during the day, shallowest at dusk, slightly deeper at night, and even deeper at dawn. Their mean depths of occurrence were between 21 and 37 m at all times. At these depths, prey (copepod nauplii) generally were at densities sufficient for larval pollock growth as determined in laboratory studies. Pronounced thermoclines and pycnoclines were present in the part of the water column inhabited by the larvae in late May. Larvae appear to remain below the upper mixed layer during periods of increased turbulence, but at depths during daytime where light was sufficient for feeding and where prey densities were adequate.

The vertical distributions and movements of planktonic organisms must be studied to understand their population dynamics. Often individual populations undergo vertical migrations and inhabit different advective and thermal regimes on a daily cycle (e.g. Hardy, 1936; Enright, 1977). The entire planktonic community may migrate similarly, or different organisms may cooccur on a diel cycle. The reasons for diel vertical migrations of ichthyoplankton may be related to feeding-digestion cycles, enhanced predator avoidance, or directed transport (Norcross and Shaw, 1984; Lampert, 1989).

Planktonic eggs of most marine fishes occur in the upper water column, although there are exceptions (Ahlstrom, 1959; Coombs et al., 1981). Neilson and Perry (1990) reviewed literature on vertical migration in fishes, particularly larvae of marine fishes, and attempted to identify common patterns and underlying causal mechanisms. They concluded that changes in depth distribution of larvae, while possibly under endogenous control, seem to be mediated by a number of environmental factors. While light and gravity dominate, other factors such as hydrography, food, tidal currents, and turbulence may also be important (Neilson and Perry, 1990; Lough and Potter, 1993). Planktonic larvae of fishes are found generally at shallower depths at night than during the day (Kendall and Naplin, 1981) although the opposite pattern also occurs (Boehlert et al., 1985; Yamashita et al., 1985; Sogard et al., 1987). In some species inconsistent patterns have been found among studies, possibly indicating the confounding effects of several biotic and

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abiotic factors (Sclafani et al., 1993). Vertical migrations in ichthyoplankton usually take place within the upper water column and may be correlated with the vertical distribution of larval fish prey (Munk et al., 1989; Pritchett and Haldorson, 1989). In some species the vertical extent of diel migrations increases as larvae grow (Ellertson et al., 1981; Yamashita et al., 1985).

In early April a large population of walleye pollock, *Theragra chalcogramma*, spawns in a restricted region of Shelikof Strait, Gulf of Alaska. The resulting planktonic eggs and larvae can be found, often in large patches, through April and May. Recruitment variation of this population has been examined, particularly those factors affecting interannual fluctuations in egg and larval mortality (Schumacher and Kendall, 1991).

Previous studies of the vertical distribution of walleye pollock eggs and larvae in Shelikof Strait have relied upon unmonitored discrete depth sampling (Kendall et al., 1987; Kendall and Kim, 1989). They have suggested that eggs occur generally below 150 m, and systematically change depth during their ~14-day incubation. Most larvae in these studies were found in the upper water column between about 10 and 50 m, but they migrated vertically. They seemed to congregate near the upper part of this range around sunrise and sunset, were situated somewhat deeper during midday, and were distributed more uniformly at night. A similar pattern for larval walleye pollock has been observed in other parts of the North Pacific (Kamba, 1977; Pritchett and Haldorson, 1989; Walline[1]).

The present study describes the vertical distribution of walleye pollock eggs and larvae in relation to changing environmental factors, measured on several dates in Shelikof Strait. This study is based on the analysis of 36 MOCNESS tows (Multiple Opening-Closing Net and Environmental Sensing System; Weibe et al., 1976) made over a period of three years. We examine ontogenetic changes in vertical distribution of eggs and larvae, and relate observed patterns to estimated ambient light and to measured temperature, salinity, and seawater density. Effects of vertical distribution of larval prey and changes in mixed layer depth due to wind events are also considered.

Materials and methods

MOCNESS tows were made from the NOAA ship *Miller Freeman* during spring 1986, 1987, and 1988, in areas where high abundance of eggs or larvae were expected (Kendall and Picquelle, 1990) and had been detected by exploratory sampling. Details of sampling during these cruises are contained in Incze et al. (1987), Proctor (1989), and Lawrence et al. (1991). Some of the tows reported here (8–11 May 1986, series four) were also used in a study of the response of zooplankton to the passage of a storm (Incze et al., 1990). On each MOCNESS tow, seven or eight nets were deployed. The nets were towed obliquely at 0.8–1.0 m/second through selected depth intervals and opened and closed in sequence. Net depth, flowmeter readings, temperature, and salinity (1987 and 1988) were displayed in real-time and digitally recorded. The nets had a nominal mouth area of 1 m^2. Volumes filtered per tow ranged from 34 to 980 m^3 (mean=167 m^3). Net mesh was 0.153, 0.333, or 0.505 mm, depending on the size range of the larvae expected as well as other sampling objectives.

Depth intervals were based on previous studies indicating that the eggs occurred primarily below 150 m and the larvae primarily in the upper 50 m (Kendall et al., 1987; Kendall and Kim, 1989). Early in the season when eggs were predominant, we focussed on the lower water column (>150 m), which was subdivided into 20-m sampling strata. Later in the season, we subdivided the upper water column (<90 m) into 15-m sampling strata.

Samples were fixed in 4–5% formalin and shipped to the Polish Plankton Sorting Center in Szczecin, Poland, where fish eggs and larvae were separated, and walleye pollock eggs and larvae were identified and counted. Stage of development of eggs was determined in each tow taken early in the season according to Blood et al. (1994). When more than 100 eggs were present in a sample, a subsample of 100 was staged. The egg stage data then were compressed into six stage groups as in Kendall and Kim (1989). Standard length (SL) (to 0.1 mm) of the larvae in each sample was measured. A subsample of 50 larvae was measured when more than 50 larvae were present in a sample. Catches of eggs and larvae per depth interval are reported as numbers per 1,000 m^3 of water based on volume filtered as determined from digital flowmeter records and net-frame angle. Mean and standard deviations (SD) of numbers per 1,000 m^3 for each tow were computed from the weighted average of the numbers per 1,000 m^3 from each net within the tow, by using the length of the depth interval for each net as the weight. Estimation of egg and larval mean depth, larval mean length, and their standard deviations is based on cluster sampling where each tow represents a cluster, each net subsamples eggs and larvae from the cluster, and each egg or larva is an element within the cluster (Equations 8.1 and 8.2 in Scheaffer et al., 1986). The observation associated

[1] Walline, P D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June–July 1979. NWAFC Processed Rep. 81-05. Northwest and Alaska Fish. Cent., NMFS, NOAA, Seattle, WA 98115-0070, 22 p.

with each egg or larva, used to estimate mean depth, is the depth of the net where it was collected. Additionally, observations of lengths of larvae in each net were used to estimate mean lengths. Gaussian statistics, including analysis of variance (ANOVA) and analysis of covariance (ANCOVA), were used to compare mean depths of eggs and larvae and stages of eggs, and lengths of larvae with various environmental variables: time of day, temperature, salinity, and depth.

Temperature and salinity data from vertical Seabird conductivity, temperature, and depth (CTD) casts made in conjunction with the MOCNESS tows in 1986 were processed at the Pacific Marine Environmental Laboratory, Seattle. CTD data were collected with Seabird sensors on the MOCNESS in 1987 and 1988 and were processed at the Atlantic Oceanographic and Meteorological Laboratory, Miami. CTD data were available at 1-m depth intervals. In comparing temperature and density (expressed as σ_t) with depths of occurrence of eggs and larvae among tows, the mean and standard deviation of temperature and density were calculated within the depth interval of +/– one standard deviation of the mean depth of eggs or larvae. Egg mean depth weighted by abundance was regressed on temperature. Meteorological data from the Kodiak airport for the sampling periods in April and May 1986, 1987, and 1988 were used to model hourly irradiance at depth in the area by using an attenuation coefficient of 0.16 (a mean value of 33 measurements [SD=0.103] made aboard ship in Shelikof Strait between 3 and 23 May 1991[2]).

[2] Davis, R. AFSC. Personal commun., April 1992.

Data from the 36 tows were grouped into nine "series" that were numbered sequentially based on calendar day without regard to year. The first time series included eggs sampled on 12–16 April, and the ninth series included larvae sampled on 23–25 May. Tows within a series were taken with the same rationale; i.e. in a fixed location or following a drogue, with similar depth schemes, and close to the same dates (Table 1). Each series was composed of one to eight tows taken in areas of high egg and/or larval concentrations except series six and seven, which were taken primarily for zooplankton studies (Fig. 1). Series eight, in mid-May, was taken about seven weeks after peak spawning, in the spawning area. Series four and nine had time series sufficient to investigate diel differences in vertical distribution. Tows during these two series were taken at local midnight (midway between sunset and sunrise), dawn (sun 20° above the horizon), local noon, and dusk (sun 20° above the horizon).

Results

Overall densities

Egg densities were highest in the first series of tows, taken between 12 and 16 April, when mean concentration in the water column based on all nets in the tows varied from 12,057 to 34,734 eggs/1,000 m^3 (SD ranged from 5,827 to 30,619). Egg densities were greater than 1,000/1,000 m^3 per tow in series two, and generally decreased as the season progressed (Table 2). Eggs were present during series three to eight through the middle of May, but in reduced con-

Table 1

Dates and tow depths for MOCNESS series used to investigate vertical distribution of walleye pollock, *Theragra chalcogramma*, eggs and larvae in the Shelikof Strait region.

					Depths (m)													
			Day of year		Net 1		Net 2		Net 3		Net 4		Net 5		Net 6		Net 7		Net 8	
Series	Date	No tows	Start	End	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
1	12–16 April 1987	3	102	106	1	50	50	100	100	150	150	170	170	190	190	210	210	230	230	250
2	21–27 April 1988	7	111	117	1	60	60	120	120	140	140	160	160	180	180	200	200	220	220	250
3	30 April–1 May 1988	3	120	121	1	20	20	40	40	60	60	80	80	100	100	150	150	200	200	255
4	8–11 May 1986	7	128	131	2	15	15	30	30	45	45	60	60	80	80	100	100	150	150	200
5	13–14 May 1986	3	133	134	2	15	15	30	30	45	45	60	60	80	80	100	100	150	150	180
6	15 May 1986	2	135	135	2	15	15	30	30	45	45	60	60	80	80	100	100	150	150	170
7	17–18 May 1986	2	137	138	1	15	15	30	30	45	45	60	60	80	80	100				
8	18 May 1986	1	138	138	1	15	15	30	30	45	45	60	60	80	80	100	100	150	150	195
9	23–25 May 1987	8	143	145	0	15	15	30	30	45	45	60	60	80	80	100	100	125	125	150
	Total tows	36																		

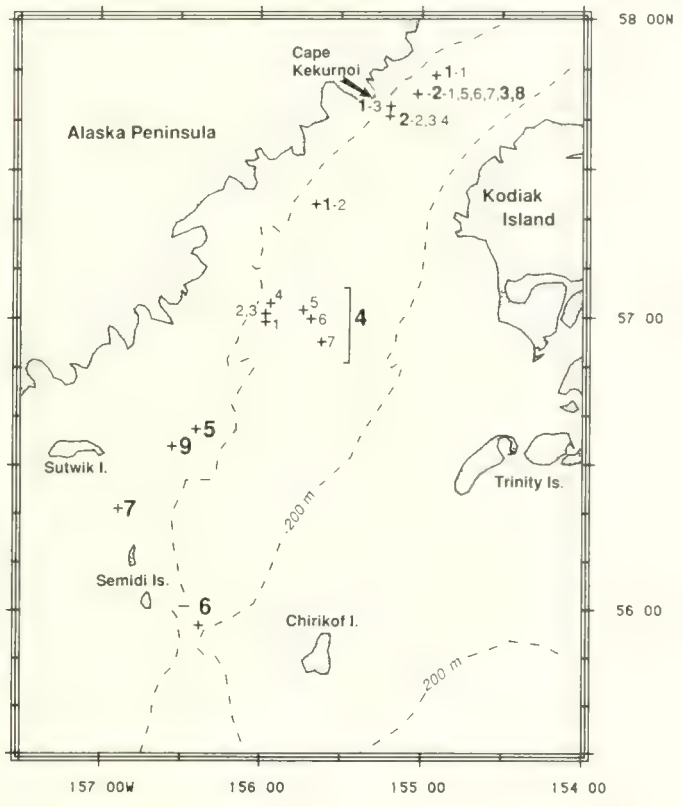

Figure 1

Locations of MOCNESS sampling series (large numbers) and tows (small numbers). Tows are shown only when there were substantial differences among their locations.

centrations, partially because sampling then was southwest of the main spawning area (Fig. 1), and partially because it was after peak spawning. The notable exception was the single tow of series eight taken in the area of maximum spawning. Although it was mid-May, egg densities were relatively high (139/1,000 m^3), indicating that some spawning had occurred within the previous two weeks.

Larvae were abundant in all series except the first when they were absent (Table 2). Mean density of larvae among the tows in series two through nine ranged from 39 to 509/1,000 m^3 (SD ranged from 54 to 1,011/1,000 m^3). Series were not always in the expected area of maximum concentration of larvae and thus do not necessarily represent the seasonal trends in larval abundance (see Kendall and Picquelle, 1990).

Series four followed a surface drifter with a drogue at 30–35 m (Incze et al., 1990), whereas sampling during series nine was at a fixed geographic location. During the 2.5 days of series four, the buoy moved anticyclonically. Catches in these two series varied considerably; during series four the mean density among tows was 82–285 larvae/1,000 m^3, compared with 42–482 larvae/1,000 m^3 during series nine (Table 2). The coefficient of variation of density among tows for series four was 0.63 and for series nine it was 0.68, indicating that variability among tows using the two sampling strategies was similar.

Overall depth distributions

Mean depths of eggs decreased during the season. Multiple comparison tests of mean depths of eggs showed significant differences between series one, two, and three, when eggs were most abundant. Among the 10 tows in the first two series, the observed mean depth of eggs was between 153 and 206 m (Fig. 2). In series three through eight, the observed mean depth was less than 130 m, but the number of eggs was relatively small. The shallower towing schemes of series four through eight may have biased the mean depth of eggs, but the general trend is thought to be real.

During the second series, when only newly hatched larvae were present, their observed mean depths of occurrence were from 165 to 212 m among tows (Fig. 3). One standard deviation of mean depth was 27 to 73 m and generally increased during the series (Fig. 3). In the third series, when recently hatched larvae dominated, larval mean depths varied from 70 to 106 m (range of SD: 83–91 m). As opposed to series two and three, when larvae were mainly found below 100 m, mean depths of larvae during series four ranged from 24 to 58 m (range of SD=15–71 m)[3]. Mean depths of occurrence of larvae from series five through seven (13–18 May 1986) varied from 15 to 47 m (range of SD=8–36 m) (Table 3). In series eight, taken in mid-May in the spawning area, the larvae averaged 4.6 mm (SD: 0.18 mm) (Table 2), and their mean depth of occurrence was 21 m (SD = 18 m). During series nine in late May, mean depths of larvae among the tows ranged from 15 to 38 m (Table 3) and varied on a diel basis (see below).

[3] Larvae in the noon tow on the second day of sampling had a mean depth of 58 m (SD=71 m). This was due to an unusually large catch in the deepest net (607/1,000 m^3 [23% of all the larvae in the tow] at 150–200 m) of larvae with a mean length of 4.71 mm. This appeared to be larger than the overall mean of the larvae collected at this depth during this series (4.35 mm), indicating the catch was not all newly hatched larvae that had not moved to the upper water column. If we discount this net, the mean depth of larvae in this tow was 21.5 m, close to the value in the other tows of the series (Fig. 4).

Changes in depth distribution with ontogeny

There was considerable variation in the mean depths of occurrence and in the abundance of eggs of different stages among the 13 tows of series one, two, and three (Table 3). Stage groups one and six were significantly deeper than stage groups three, four, and five; stage group two was intermediate in depth (Fig. 5) (ANOVA, multiple comparisons test $P<0.05$).

Almost all of the larvae collected deeper than 100 m throughout the study were <5 mm, while the length of larvae in the upper part of the water column appeared to increase later in the season (Fig. 6). In several tows of series four through eight, a bimodal depth distribution was evident; most larvae were found in the upper 60 m, almost no larvae found between 60 and 100 m, and larvae again were present deeper than 100 m. Mean lengths of larvae in the nets of the tows of series nine ranged from 4.8 to 9.8 mm, with an overall mean of 7.8 mm. There was no indication of length stratification of larvae within the upper 100 m. The mean lengths of larvae among tows in series nine were relatively homogeneous (7.2–8.6 mm).

Table 2

Mean density (number/1,000 m^3) and standard deviation (SD) of density by tow of walleye pollock, *Theragra chalcogramma*, eggs and larvae, and mean and standard deviation of larval lengths (mm SL) from MOCNESS tows.

		Density (no./1,000 m^3)					
		Eggs		Larvae		Larval length (mm SL)	
Series	Tow	Mean	SD	Mean	SD	Mean	SD
1	1	19,994	14,317.2				
1	2	12,057	5,827.0				
1	3	34,734	30,618.6				
2	1	1,509	833.3	168	271.6	3.8	0.04
2	2	3,543	3,204.0	90	89.5	3.7	0.06
2	3	2,402	1,858.9	89	90.0	3.9	0.10
2	4	1,270	804.1	230	257.8	3.8	0.06
2	5	3,641	2,489.5	322	253.2	4.1	0.04
2	6	3,276	1,696.2	389	296.1	3.6	0.04
2	7	2,333	791.3	341	316.6	3.7	0.07
3	1	411	207.6	341	444.2	4.7	0.08
3	2	671	565.3	208	163.8	4.0	0.09
3	3	779	801.3	304	331.8	4.3	0.07
4	1	52	33.4	82	88.1	5.0	0.09
4	2	77	87.1	105	130.6	4.9	0.08
4	3	98	100.7	183	288.8	4.7	0.11
4	4	124	190.6	285	449.4	5.1	0.09
4	5	170	333.2	152	228.6	5.7	0.11
4	6	204	342.4	148	199.0	5.1	0.09
4	7	59	85.0	232	261.3	5.7	0.07
5	1	26	23.7	423	696.8	5.6	0.09
5	2	40	50.2	509	770.6	5.8	0.08
5	3	24	12.9	114	121.3	5.4	0.09
6	1	5	5.0	355	497.1	6.0	0.08
6	2	7	9.1	419	833.7	6.1	0.10
7	1	14	16.1	39	58.8	6.7	0.18
7	2	5	7.7	53	91.6	6.3	0.10
8	1	139	96.7	109	184.5	4.6	0.18
9	1			42	53.5	7.7	0.50
9	2			475	822.4	7.9	0.13
9	3			181	384.8	8.6	0.16
9	4			208	482.7	7.2	0.12
9	5			78	125.1	8.2	0.17
9	6			256	385.5	7.7	0.14
9	7			182	1,011.4	7.5	0.16
9	8			396	639.5	8.5	0.11

Relationship of depth distribution and hydrography

The temperature of the water column measured concurrently with the tows in series one through three increased with depth from about 4.0° to 5.0°C near the surface to 5.0° and 5.5°C at 150–250 m, where most of the eggs occurred (there is no hydrographic data from tows 3 and 5 of series two). Temperature at the mean depth of occurrence of eggs varied from 4.7° to 5.4°C among the tows in series one through three (Fig. 7A). Since temperature increased with depth, among the tows of series one through three there was a positive linear relationship between mean depth of occurrence of eggs and temperature ($P<0.001$, $r^2=0.7619$). The relationship between the depth distribution of eggs and water density among tows of series one through three was not significant ($P=0.632$) (Fig. 7B).

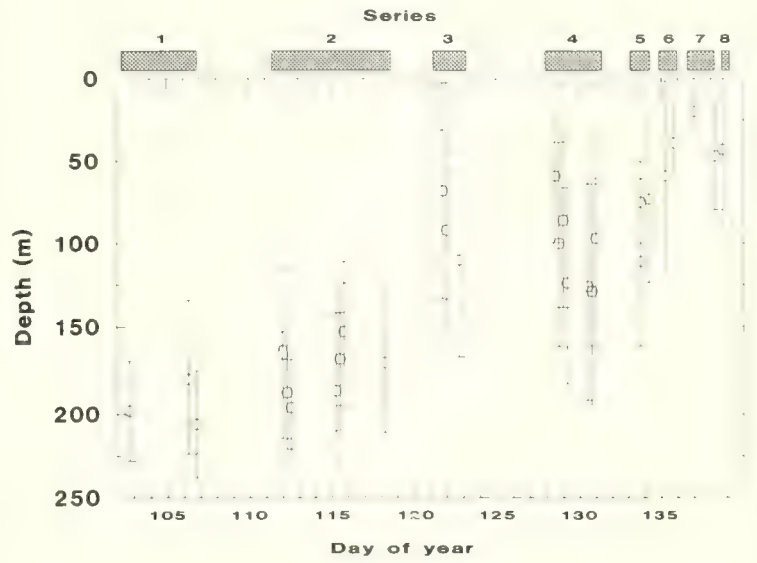

Figure 2

Eggs of walleye pollock, *Theragra chalcogramma*. Depth of occurrence by day of year and tow series number. Mean and standard deviation of the mean are shown for each tow.

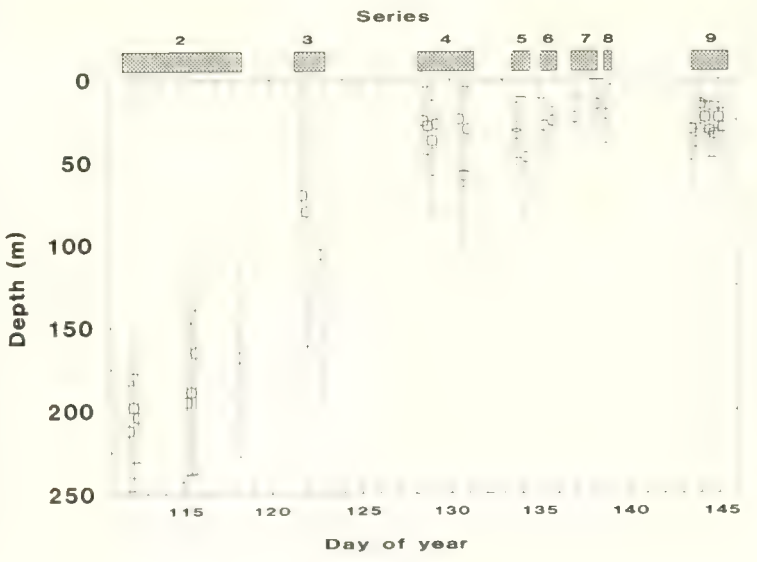

Figure 3

Larvae of walleye pollock, *Theragra chalcogramma*. Depth of occurrence by day of year and tow series number. Mean and standard deviation of the mean are shown for each tow.

When pollock larvae were first present in April as hatchlings in the lower part of the water column, they experienced temperatures of 4.9° to 5.3°C (Fig. 8). When the larvae first reached the upper part of the water column they experienced lower temperatures (~3.6°C during series four), but temperature at the mean depth of larval occurrence increased to about 5.7°C during series nine (Fig. 8).

Temperatures during series nine decreased with depth from about 6.2°C at the surface to just above

Table 3

Means and standard deviations (SD) of depths of walleye pollock, *Theragra chalcogramma*, eggs (total and by stage group) and larvae from MOCNESS tows.

				Eggs by stage group													
		Total eggs		Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Larvae	
Series	Tow	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	1	198	29.9	209	19.4	207	23.9	194	30.0	182	44.7	173	47.6	197	25.9		
1	2	179	44.8	180	31.0	174	45.6	174	51.9	183	51.2	196	51.7	200	44.9		
1	3	206	32.1	214	19.2	207	27.4	196	44.0	168	54.2	195	41.0	156	41.2		
2	1	164	50.5	161	33.2	158	48.5	156	59.6	155	54.1	158	45.7	199	42.3	212	27.9
2	2	187	33.9	179	22.4	182	27.6	193	35.1	191	36.1	184	36.5	200	35.4	198	49.8
2	3	196	28.9	196	16.9	189	24.1	191	34.7	198	31.1	199	30.1	203	30.1	204	26.6
2	4	186	44.1	177	21.9	181	25.3	163	52.0	140	65.1	177	49.2	210	33.5	195	47.6
2	5	167	43.0	206	14.2	167	36.2	143	28.8	127	38.8	144	39.4	193	34.0	189	49.5
2	6	153	42.0	193	23.2	158	47.1	145	37.3	146	37.4	143	39.7	187	40.6	165	72.7
2	7	169	42.0	184	24.9	167	31.1	159	32.6	166	49.8	159	40.1	186	46.7	168	59.7
3	1	68	65.5	144	54.6	95	66.9	54	73.3	37	40.0	56	43.6	101	77.0	70	91.1
3	2	92	60.9	133	33.4	68	52.4	84	67.8	76	46.9	92	49.1	77	67.7	80	82.7
3	3	110	55.7	84	68.8	129	56.1	94	65.5	90	47.6	102	44.8	130	51.7	106	88.9
4	1	59	40.4													25	20.5
4	2	100	61.7													28	30.1
4	3	86	52.7													37	48.3
4	4	124	57.9													27	14.5
4	5	126	65.6													24	40.9
4	6	129	65.2													58	70.5
4	7	97	64.2													30	25.7
5	1	75	24.7													29	18.6
5	2	111	50.4													33	19.0
5	3	73	50.6													47	36.2
6	1	59	57.6													28	16.5
6	2	39	24.3													25	8.0
7	1	20	11.2													23	12.3
7	2	47	32.7													15	14.8
8	1	43	47.2													21	17.7
9	1															30	36.4
9	2															38	10.9
9	3															15	15.4
9	4															23	9.6
9	5															31	16.6
9	6															33	14.3
9	7															23	8.8
9	8															29	11.3

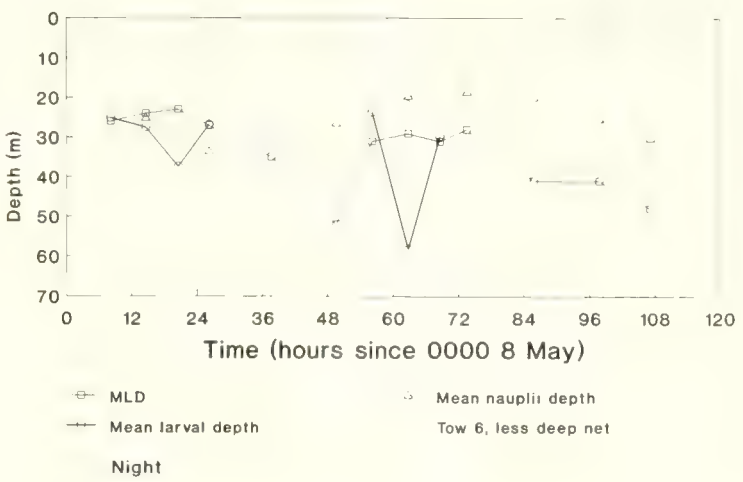

Figure 4

Time series of mixed layer depth, mean depth of copepod nauplii, and mean depth of walleye pollock, *Theragra chalcogramma*, larvae starting at 0000 hours, 8 May GMT. Mean depth of larvae excluding the catch in the deepest net of tow 6 also is plotted (see Results: overall depth distribution). Nighttime is shown by stippling near the top border.

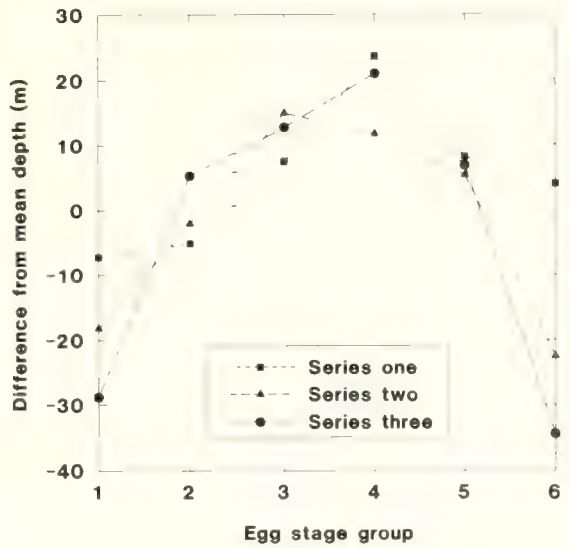

Figure 5

Vertical distribution of walleye pollock, *Theragra chalcogramma*, eggs by developmental stage group from series one, two, and three. Differences in mean depth of each stage group from mean depth of all eggs in a series are plotted.

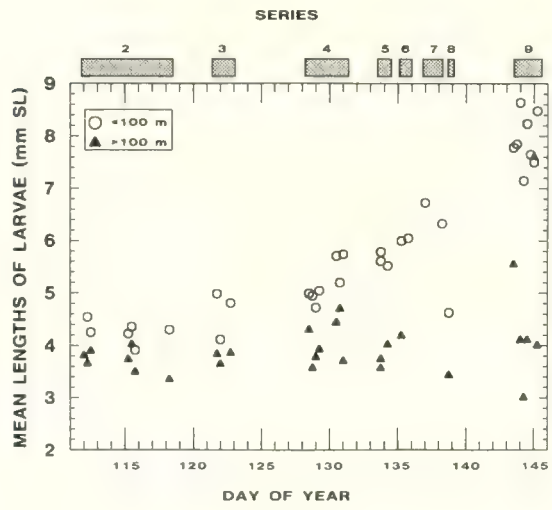

Figure 6

Standard lengths (SL) of walleye pollock, *Theragra chalcogramma*, larvae in tows above and below 100 m by day of year and tow series number.

5.0°C from about 60 m to the bottom (Fig. 9). There was a gradual thermocline between 10 and 40 m, and most of the larvae were present in or above this feature. Salinity during this series showed a gradual increase with depth from about 31.7 ppt at the surface to 32.2 ppt at 140 m. Density increased steadily from a σ_t of 24.85 at the surface to 25.25 at 60 m and 25.45 at 140 m (Fig. 9).

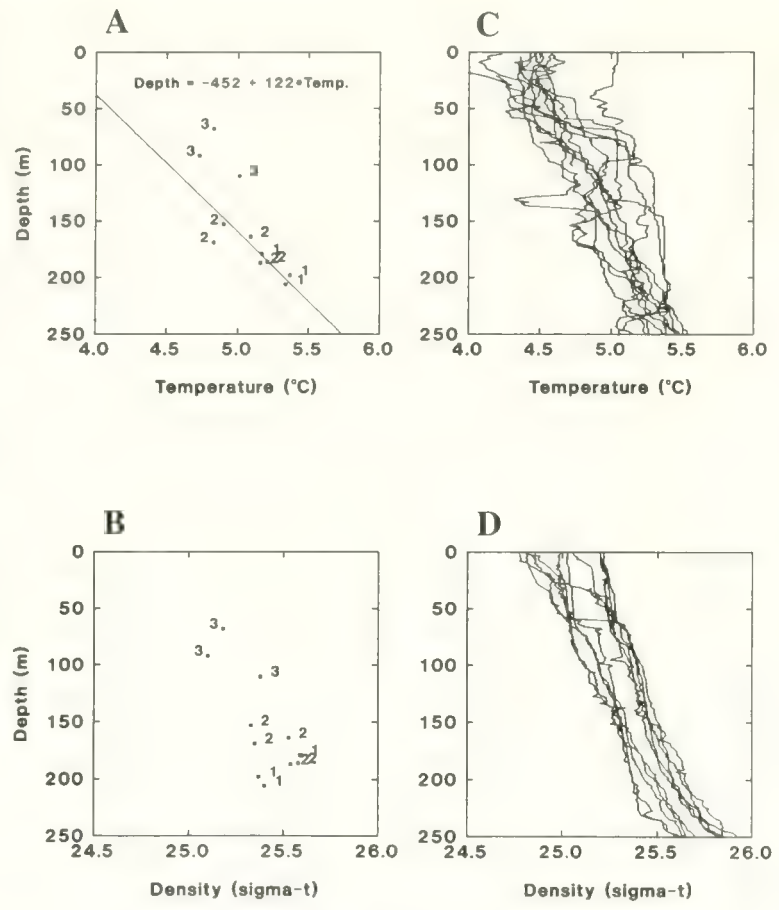

Figure 7

Mean depth of occurrence of walleye pollock, *Theragra chalcogramma*, eggs in series one, two, and three in relation to temperature (**A**) and density (**B**). Series numbers are indicated next to data points. Temperature (**C**) and density (**D**) profiles during series one, two, and three.

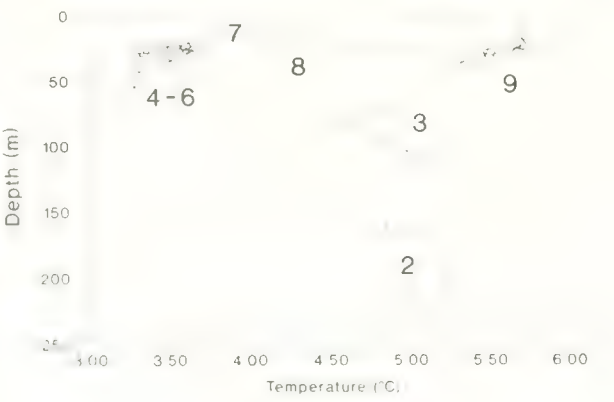

Figure 8

Mean depth of occurrence of walleye pollock, *Theragra chalcogramma*, larvae by tow in relation to temperature. Series numbers are near appropriate data points.

Diel changes in larval depth distribution

There was no clear diel pattern in the depth distribution of 5–6 mm larvae in series four (Fig. 4). During the first diel sampling period the mean depths varied from 25 to 37 m; the deepest mean depth occurred at dusk. During the second diel period, night was not sampled and an aberrant catch occurred during the noon sampling period (discussed above). The mean depths varied from 24 to 58 m, if the catch in the deep net of the noon tow is included, and from 21 to 30 m if that catch is excluded.

When proportions of larvae at each depth from series nine are examined, a clear pattern of vertical distribution emerges despite differences in overall density among tows. Although the deepest stratum sampled was 125–150 m, mean depths of occurrence of larvae were between 14.6 and 38.1 m (range of one SD=8.8–36.4 m), and fewer than 1% of all larvae were collected below 60 m. Within the upper 60 m, the larvae showed evidence of limited diel vertical migrations (Fig. 10). The observed mean depth of larvae was greater at noon than at other times (38 m and 33 m) and shallowest at dusk (15 m and 23 m). At night the larvae were found somewhat deeper (23 m and 29 m). Like the dusk sampling, the distribution at night appeared deeper during the second day compared with the first. At dawn the larvae were found between the night and noon depths (30 m and 31 m).

Although the same pattern of changes in vertical position of the larvae was observed during both 24-hour periods of series nine, differences in observed mean depths between various times of day were consistently greater on the first day than on the second (Fig. 10). The average difference in mean depth between sequential time periods on the first day was 13.2 m versus 6.2 m on the second (Table 4). The mean depths at dawn on the two days were within a meter of each other, but at the other sampling times there were differences of 4.8–8.4 m between mean depths on the two days at the same time of day. Differences were especially pronounced at dusk and night. Examination of standard deviations of mean depth and mean lengths of larvae among tows of series nine showed no consistent pattern of differences with any of the variables under consideration (time of day, depth, day).

Response of larvae to wind events and prey distributions

Increasing winds after 60 hours of sampling during series four prevented further MOCNESS tows, but other observations continued during the storm and documented the deepening of the mixed layer and subsequent changes in microzooplankton distribution (Incze et al., 1990). The path of the drogue, the sequence of CTD data obtained in the area, and limited satellite imagery suggested the presence of an anticyclonic eddy (Incze et al., 1990; Nieman[4]). The mixed layer depth during the first half of series four was variable, but during the last half it deepened, presumably in response to increased winds (Fig. 4). Copepod nauplii of length range 150–350 µm, which has been found to be the size range primarily eaten by 5–6 mm walleye pollock larvae (Paul et al., 1991), had mean depths between 20 and 34 m during series four (Fig. 4). Their observed mean depth increased during the storm, but their densities at some depth within the upper 45 m was always greater than 15 per liter. Excluding the deep net from the noon tow on day two, the mean depths of larvae in series four were at or 5–10 m below the mixed layer depth and the mean depth of 150–350 µm copepod nauplii.

Wind, measured hourly aboard the ship during series nine, increased from less than 8 m/second during the first six tows of this series to over 12 m/second by the end of the series. The mixed layer was about 25 m deep at the time of the last tow (night) in series nine as opposed to about 10 m during the previous seven tows (Fig. 9). The greater mean depths of larvae at dusk and night on the second day of sampling compared with the first day of sampling were possibly caused by increased turbulence and deepening of the mixed layer (Fig. 10).

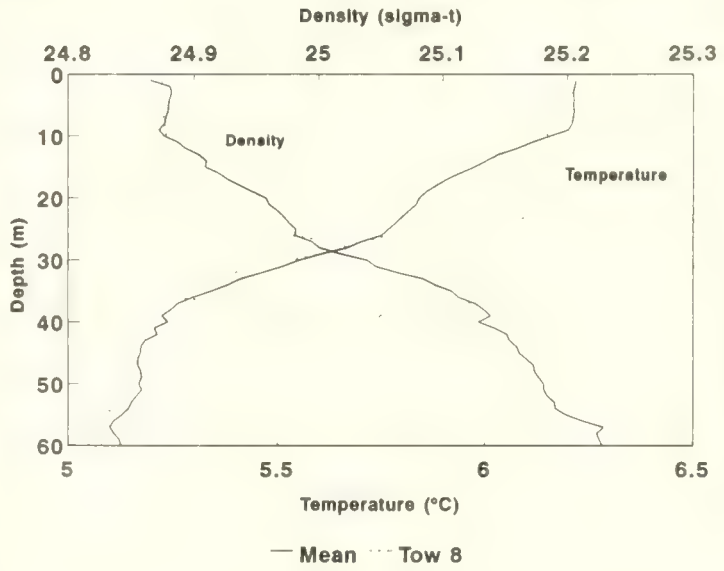

Figure 9

Temperature and density profiles from series nine. Profiles of means of all tows and from tow eight, showing deepening of the mixed layer (see Results: response of larvae to wind events and prey distributions), are plotted.

Table 4

Comparisons (means and standard deviations [SD]) of walleye pollock, *Theragra chalcogramma*, larvae by depth (m), length (mm SL) and density (no./1,000 m^3) in series nine at four times of day (dawn, noon, dusk, and night).

		Depth (m)		Length (mm SL)		Density (no./1,000 m^3)	
Tow	Time	Mean	SD	Mean	SD	Mean	SD
1	dawn	30	36.4	7.7	0.50	42	54
2	noon	38	10.9	7.9	0.13	475	822
3	dusk	15	15.4	8.6	0.16	181	385
4	night	23	9.6	7.2	0.12	208	483
5	dawn	31	16.6	8.2	0.17	78	125
6	noon	33	14.3	7.7	0.14	256	386
7	dusk	23	8.8	7.5	0.17	482	1,011
8	night	29	11.3	8.5	0.11	396	640
	dawn	30.6		8.06		33.6	
	noon	36.6		7.79		249.6	
	dusk	21.4		7.72		228.4	
	night	27.0		8.09		150.7	
	day 1	26.4		7.84		124.9	
	day 2	29.0		7.97		156.2	

Discussion

Most walleye pollock eggs in Shelikof Strait developed at depths between 150 and 200 m. However, there was considerable variation in the mean depth of eggs among the tows. Mean depth of eggs varied from 153 to 206 m in April (when egg densities were high) and from 20 to 129 m in

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May. Although many factors probably contributed to the distribution of eggs, their distribution was positively related to temperature, which increased with depth.

Kendall and Kim (1989) developed a model, based on field collections and laboratory experiments, to describe the vertical distribution of walleye pollock eggs from Shelikof Strait in relation to water density. One of the model's assumptions was that the specific gravity of eggs does not vary interannually. Based on this assumption and their observations of the changes in egg buoyancy and depth distribution during development, eggs would rise to different depths in the middle stages of development depending on water density in particular years. The vertical distribution might then influence the horizontal distribution of eggs if there was a significant vertical shear in the water column. Like Kendall and Kim (1989), we found middle-stage pollock eggs at shallower depths than early or late stage eggs. Our data, however, suggest that the depth distribution of eggs changes during development regardless of water density. Pollock egg density appears to vary interannually—in the eight tows from which significant numbers of eggs were collected and for which concurrent hydrographic data are available, the mean depth of occurrence varied from 153 to 206 m, and the density varied from 25.31 σ_t to 25.63 σ_t. Among the four years for which Kendall and Kim (1989) present data (1977, 1981, 1985, 1986), density in the middle layer of the water column (162–216 m) varied interannually from 25.58 σ_t to 25.87 σ_t, and modelled depth distribution of middle-stage eggs varied from about 160 to 230 m. While the ranges of density and depth of eggs seen in the present study are similar to those modelled by Kendall and Kim (1989), the proposed relationship between depth of eggs and water density is not evident. A relationship might have been seen if a greater range of water densities had been found. The temperature and density of the water in which most of the eggs were found in the present study (1987 and 1988) most closely resembled the values reported for 1981 by Kendall and Kim (1989).

Ingraham et al. (1991) compared long-term annual means of water temperature, salinity, and density at 225 m depth in Shelikof Strait with values in individual years when circulation in the Gulf of Alaska was anomalous. They found high values for all three variables in 1985; this was a year when water on the continental slope did not include fresher, colder waters from the eastern Gulf of Alaska owing to reduced westward transport. Of the years considered here (1985–88), only 1985 was characterized by anomalous flow conditions that could have produced unusually warm, dense (>5.4°C, >26.2 σ_t) bottom water in Shelikof Strait (Ingraham et al., 1991). According to the model in Kendall and Kim (1989), the eggs should have risen closest to the surface in 1985. However, mean depth of eggs in the four tows in 1985 was 220 m, in the five tows in 1986 it was 211 m (Kendall and Kim, 1989), in the three tows of series one in 1987 it was 200 m, and in the seven tows of series two in 1988 it was 176 m.

In series three through eight, the mean depth of occurrence of eggs was less than 130 m. Given the low numbers of eggs and the sampling intervals designed mainly to sample larvae, these values are not robust. Kendall and Kim (1989) also found some eggs with significantly lower density than others in their specific gravity experiments. The data presented here confirm that some eggs have a low specific gravity value, but that these are infrequent and occur primarily later in the season after the majority of eggs have hatched.

Apparently after hatching, larvae move quickly to the upper part of the water column. Both eggs and larvae in series two had mean depths of occurrence between 153 and 212 m among the seven tows. The mean length of larvae in series two was 3.8 mm, which is within the range of size at hatching (Kendall

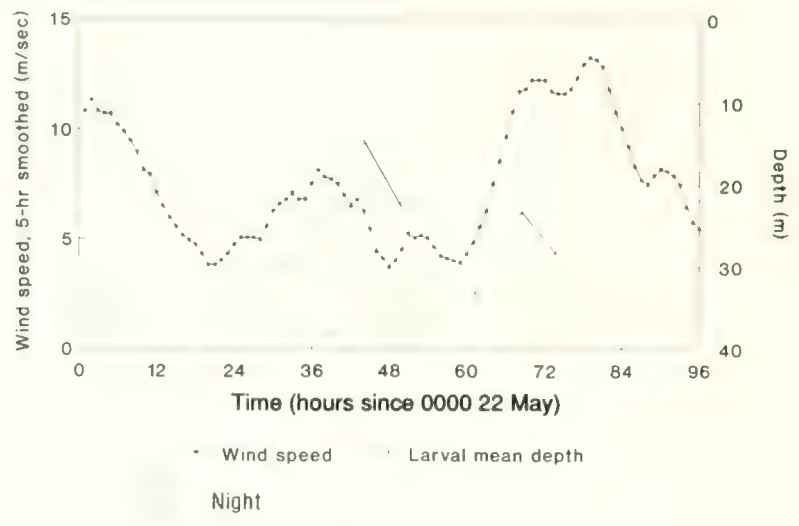

Figure 10

Mean depth of walleye pollock, *Theragra chalcogramma*, larvae and wind speed during series nine.

et al., 1987). In series three, the mean depths of occurrence of eggs and larvae decreased to between 68 and 110 m, and the mean length of larvae increased to 4.4 mm, indicating that growth of some pollock larvae had occurred (SD of length was 0.18 in series three as opposed to 0.09 in series two). The standard deviations of depth of larval occurrence in series three (83 to 91 m) were larger than in any other series, suggesting that these larvae were in transition from the deep hatching environment to shallower levels. Although larvae respond positively to light within 24 hours of hatching, their negative geo/barotaxis may enable them to reach the upper layers since insufficient light for response penetrates to hatching depths (see Olla and Davis, 1990). The relatively shallow mean depth of eggs in series three also may account for the large variation in larval depth during that series. Older larvae from eggs at the depths observed during series two (>150 m) could have mixed with larvae hatching from eggs found at the depths observed during series three (<110 m). The larger standard deviation of larval length in series three compared with series two supports this explanation. In later series the mean depth of occurrence of the larvae was less than 60 m, and the standard deviation generally was less than 20 m. Once they reach the upper layers, vertical movements increase as larvae develop. No significant diel migrations were noted in series four, as opposed to the pattern seen in series nine. The mean length of larvae in series four was 5.3 mm; in series nine it was 7.9 mm. The larvae sampled by Kendall et al. (1987) in late May were 11.0 mm long and demonstrated a pattern of vertical distribution similar to the larvae collected here in series nine.

During series nine, larvae followed a diel (crepuscular) pattern of vertical movements in which they ranged deepest at noon, shallowest at dusk, and progressively deeper through the following noon. Although this pattern was observed on both days, the amplitude of movements were reduced on the second day. However, the wind had markedly increased by evening of the second day. Larvae may have been avoiding the turbulent surface on the second day when their mean depths were deeper. Olla and Davis (1990) found that pollock larvae avoid turbulence in the laboratory.

The relationships of larval fish feeding, growth, and survival to storms and turbulence have been the subject of numerous studies (e.g. see Sundby and Fossum, 1990; Maillet and Checkley, 1991). Both positive and negative effects have been postulated and observed. Positive effects of increased turbulence include hypothesized enhanced encounter rates between larvae and their prey (Rothschild and Osborn, 1988), and enhanced primary production after mixing has ceased owing to infusion of nutrients from below the photic zone. Negative impacts include dilution of vertically enriched layers of prey to levels below successful feeding thresholds and reduced naupliar production in lower phytoplankton concentrations (Lasker, 1978). There is evidence that in Shelikof Strait, below-average walleye pollock production may result if strong wind events occur when larvae are at the first-feeding stage.[5] Incze et al. (1990) found that naupliar concentrations remained above feeding threshold levels during the passage of a storm, but this was a relatively transient phenomenon. The present study indicates that larvae may avoid upper layer turbulence by moving deeper in the water column. If so, they might experience prey densities or light levels too low for optimal feeding.

In a 24-hour study of the vertical distribution of pollock larvae in Auke Bay, Alaska (average depth 60 m), Pritchett and Haldorson (1989) found larvae congregated at 10 m at noon, at 5 m at dawn and afternoon, and at 15–20 m at night. At twilight (0.3 hour before sunrise, 1.5 hours before sunset), larvae were more dispersed, seen mostly at 10 m near sunrise and at 15 m near sunset. The vertical extent of diel migration increased with larval length. In the present study, depths of occurrence were greater at all times than those reported by Pritchett and Haldorson (1989), and noon depths of larger larvae were greater than the night depths. However, in both studies, larvae were found to be deeper at noon than at dawn and dusk, and a relationship between vertical migration and larval length was seen. The depth distribution of copepod nauplii in Auke Bay usually centered around 5–10 m (Paul et al., 1991). Inzce et al. (1990) reported maximum densities of copepod nauplii in the upper 30 m of Shelikof Strait when pollock larvae are abundant. Since nauplii are the primary prey for pollock larvae, the larvae may well adjust their daytime feeding depths to correspond to those of the nauplii. Alternatively, the greater daytime depth of pollock larvae in Shelikof Strait may be related to the greater depth of light penetration in Shelikof Strait compared with Auke Bay (Zeimann et al., 1990).

Light is frequently cited as a factor controlling the depth of occurrence for fish larvae. Larvae of some species follow the common trend of rising toward the surface at night and of remaining deeper during the day (Smith et al., 1978; Kendall and Naplin, 1981; Davis et al., 1990). Other species follow an opposite pattern, ranging deeper at night than by day (Boeh-

[5] Bailey, K. M., AFSC, and S. A. Macklin, Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE., Seattle, Washington 98115-0070. Personal commun., February 1993.

lert et al., 1985; Yamashita et al., 1985; Sogard et al., 1987; Davis et al., 1990). Fewer studies have examined the vertical distribution of fish larvae during crepuscular periods. The present study has shown that larger larval pollock range deeper during the day than at night and that, at dawn and dusk, they are present at shallower depths in the water column than at midday. We hypothesize that these changes in vertical position allow pollock larvae to extend the length of their daily feeding period.

In the laboratory, first-feeding pollock larvae could not feed at light levels below 0.006 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Paul, 1983). Except at night, light levels are brighter than those at the depths where we found feeding-stage larvae. In studies of behavioral responses of walleye pollock larvae (4–8 mm SL) to light in the laboratory, Olla and Davis (1990) found reduced activity and orientation in a nonfeeding mode at light levels <0.01 and avoidance of light at levels >13 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In the dark, larvae migrated upward and remained in the upper part of the chambers, demonstrating negative geotaxis or barotaxis, or both. Light levels between 0.01 and 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ are estimated to have occurred between about 25 and 60 m during our sampling in Shelikof Strait. The mean depths of feeding larvae were typically in the upper part of this range (Fig. 11). Larvae longer than 7 mm seemed to adjust their vertical position on a diel cycle to stay at light levels similar to those "preferred" in the laboratory. At night these larvae were present at depths where light had been greater than 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during the day.

The relationship of vertical distribution of larval fish to vertical temperature structure of the water column varies among species (Kendall and Naplin, 1981; Sogard et al., 1987). Hypothetically, there are metabolic advantages to diel descents into cooler waters (Lampert, 1989). Larvae that stay nearer the surface (at higher temperatures) at night when they are digesting their food may accrue such advantages (Wurtsburgh and Neverman, 1988). However, given the small differences in temperature with depth observed here (~1°C), energetic advantages are almost certainly insignificant compared with the advantages of feeding at optimal light levels and at depths of maximum prey abundance. An alternative advantage of residing deeper, and thus at lower light levels during daytime, may be to avoid visual predators.

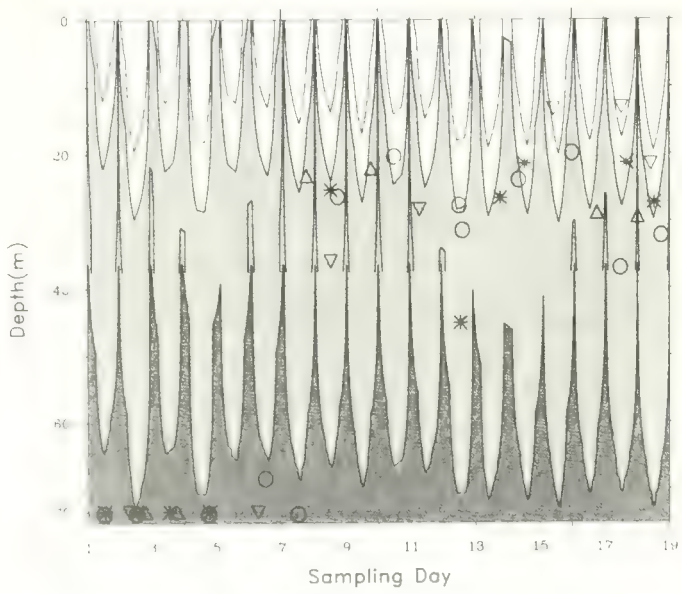

Figure 11

Predicted light levels at depth on days of sampling and mean depths of walleye pollock, *Theragra chalcogramma*, larvae in MOCNESS tows (indicated by circles for daytime tows, triangles pointed down for dusk tows, asterisks for night tows, and triangles pointed up for dawn tows). Depths of three light levels are plotted: 50, 10 and 0.01 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Light levels above 50 are clear, those 10–50 are light gray, those 0.01–10 are medium gray, and those less than 0.01 $\mu mol \cdot m^{-2} \cdot s^{-1}$ are dark gray. Light levels are based on incident light at the Kodiak airport during the sampling periods with an extinction coefficient of 0.16.

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Literature cited

Ahlstrom, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fish. Bull. 60:107–146.

Blood, D. B., A. C. Matarese, and M. M. Yoklavich.
1994. Embryonic development of walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull. 92:207–222.

Boehlert, G. W., D. M. Gadomski, and B. C. Mundy.
1985. Vertical distribution of ichthyoplankton off the Oregon Coast in spring and summer months. Fish. Bull. 83:611–621.

Coombs, S. H., R. K. Pipe, and C. E. Mitchell.
1981. The vertical distribution of eggs and larvae of blue whiting (*Micromesistius poutassou*) and mackerel (*Scomber scombrus*) in the eastern North Atlantic and North Sea. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:188–195.

Davis, T. L. O., G. P. Jenkins, and J. W. Young.
1990. Diel patterns of vertical distribution in larvae of southern bluefin *Thunnus maccoyii* and other tuna in the East Indian Ocean. Mar. Ecol. Prog. Ser. 59:63–74.

Ellertson, B., P. Solemdal, S. Sundby, S. Tilseth, T. Westgard, and V. Oiestad.
1981. Feeding and vertical distribution of cod larvae in relation to availability of prey organisms. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:317–319.

Enright, J. T.
1977. Diurnal vertical migration: adaptive significance and timing. Part 1: Selective advantage: a metabolic model. Limnol. Ocean. 22:856–872.

Hardy, A. C.
1936. Plankton ecology and the hypothesis of animal exclusion. Proc. Linn. Soc. Lond. 148:64–70.

Ingraham, W. J., Jr., R. K. Reed, J. D. Schumacher, and S. A. Macklin.
1991. Circulation variability in the Gulf of Alaska. EOS, Trans. Am. Geophys. Soc. 74:257–264.

Incze, L. S., J. Gray, J. D. Schumacher, A. W. Kendall Jr., K. M. Bailey, and S. A. Macklin.
1987. Fisheries-Oceanography Coordinated Investigations (FOCI) field operations—1986. NOAA Data Report ERL PMEL-20, 64 p.

Incze, L. S., P. B. Ortner, and J. D. Schumacher.
1990. Microzooplankton, vertical mixing and advection in a larval fish patch. J. Plankton Res. 12:365–379.

Kamba, M.
1977. Feeding habits and vertical distribution of walleye pollock, *Theragra chalcogramma* (Pallas), in early life stage in Uchiura Bay, Hokkaido. Res. Inst. N. Pac. Fish., Hokkaido Univ., Spec. Vol., p. 175–197.

Kendall, A. W., Jr., and N. A. Naplin.
1981. Diel-depth distribution of summer ichthyoplankton in the Middle Atlantic Bight. Fish. Bull. 79:705–726.

Kendall, A. W., Jr., and S. Kim.
1989. Buoyancy of walleye pollock (*Theragra chalcogramma*) eggs in relation to water properties and movement in Shelikof Strait, Gulf of Alaska. *In* R. J. Beamish and G. A. McFarlane (eds.), Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, p. 169–180. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Kendall, A. W., Jr., and S. J. Picquelle.
1990. Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Fish Bull. 88:133–154.

Kendall, A. W., Jr., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert.
1987. Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull. 85:499–521.

Lampert, W. H.
1989. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. 3:21–27.

Lasker, R.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 173:212–230.

Lawrence, L. A., J. Gray, and J. D. Schumacher.
1991. Fisheries-Oceanography Coordinated Investigations field operations—1987. NOAA Data Rep. ERL PMEL-28, 61 p.

Lough, R. G., and D. C. Potter.
1993. Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. Fish Bull. 91:281–303.

Maillet, G. L., and D. M. Checkley Jr.
1991. Storm-related variation in growth rate of otoliths of larval Atlantic menhaden *Brevoortia tyrannus*: a time series analysis of biological and physical variables and implications for larva growth and mortality. Mar. Ecol. Prog. Ser. 79:1–16.

Munk, P., T. Kiorboe, and V. Christensen.
1989. Vertical distribution of herring, *Clupea harengus*, larvae in relation to light and prey distribution. Environ. Biol. Fish. 26:87–96.

Neilson, J. D., and R. I. Perry.
1990. Diel vertical migrations of marine fishes: an obligate or facultative process? Adv. Mar. Biol. 26:115–168.

Norcross, B. L., and R. F. Shaw.
1984. Oceanic and estuarine transport of fish eggs and larvae: a review. Trans. Am. Fish. Soc. 113:153–165.

Olla, B. L., and M. W. Davis.
1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser. 63:105–112.

Paul, A. J.
1983. Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae, *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 13:175–179.

Paul, A. J., K. O. Coyle, and L. Haldorson.
1991. Interannual variations in copepod nauplii prey of larval fish in an Alaskan Bay. ICES J. Mar. Sci. 48:157–165.

Pritchett, M., and L. Haldorson.
1989. Depth distribution and vertical migration of larval walleye pollock (*Theragra chalcogramma*). *In* Proceedings of the international symposium on the biology and management of walleye pollock; 14–16 November 1988, Anchorage, AK, p. 173–183. Alaska Sea Grant Rep. 89–1, Univ. Alaska, Fairbanks.

Proctor, P. D.
1989. Fisheries-Oceanography Coordinated Investigations—field operations 1988. NOAA Data Report ERL PMEL-25, 69 p.

Rothschild, B. J., and T. R. Osborn.
1988. Small-scale turbulence and plankton contact rates. J. Plankton Res. 10:465–474.

Scheaffer, R. L., W. Mendenhall, and L. Ott.
1986. Elementary survey sampling. Duxbury Press, Boston, MA, 324 p.

Schumacher, J. D., and A. W. Kendall Jr.
1991. Some interactions between young walleye pollock and their environment in the western Gulf of Alaska. CalCOFI Rep. 32:22–40.

Sclafani, M., C. T. Taggart, and K. R. Thompson.
1993. Condition, buoyancy and the distribution of larval fish: implications for vertical migration and retention. J. Plankton Res. 15:413–435.

Smith, W. G., J. D. Sibunka, and A. Wells.
1978. Diel movements of larval yellowtail flounder, *Limanda ferruginea*, determined from discrete depth sampling. Fish. Bull. 76:167–178.

Sogard, S. M., D. E. Hoss, and J. J. Govoni.
1987. Density and depth distribution of larval Gulf menhaden, *Brevoortia patronus*, Atlantic croaker, *Micropogonias undulatus*, and spot, *Leiostomus xanthurus*, in the northern Gulf of Mexico. Fish. Bull. 85:601–609.

Sundby, S., and P. Fossum.
1990. Feeding conditions of Arcto-Norwegian cod larvae compared with the Rothschild-Osborn theory on small-scale turbulence and plankton contact rates. J. Plankton Res. 12:1153–1162.

Weibe, P. D., K. H. Burt, S. H. Boyd, and A. W. Morton.
1976. A multiple opening/closing net and environmental sensing system for zooplankton. J. Mar. Res. 34:313–326.

Wurtsburgh, W. A., and D. Neverman.
1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. Nature 333:846–848.

Yamashita, Y., D. Kitagawa, and T. Aoyama.
1985. Diel vertical migration and feeding rhythm of the larvae of the Japanese sand-eel *Ammodytes personatus*. Bull. Japan. Soc. Sci. Fish. 51:1–5.

Zeiman, D. A., L. D. Conquest, K. W. Fulton-Bennett, and P. K. Bienfange.
1990. Interannual variability in the physical environment of Auke Bay, Alaska. *In* D. A. Ziemann and K. W. Fulton-Bennett (eds.), APPRISE-interannual variability and fisheries recruitment, p. 99–128. The Oceanic Institute, Honolulu, HI.

Abstract.—Otoliths, scales, dorsal spines, and pectoral-fin rays were compared to ascertain the best hardpart for determining the age of weakfish, *Cynoscion regalis*. Each showed concentric marks, which could be interpreted as annuli. Sectioned otoliths, however, consistently showed the clearest marks, had 100% agreement between and within readers, and were validated by the marginal increment method for ages 1–5. This validated method of ageing weakfish was then compared with the traditionally used scale method. The scale method was less precise, as demonstrated by lower percent agreement, and generally assigned younger ages for fish older than age 6 (as determined by otoliths). Consequently, mean sizes at age based on scales showed no clear signs of an asymptote, whereas those based on otoliths did. Otolith annuli formed in April and May, whereas scale annulus formation was more variable, ranging from April to August. This extended time of annulus formation made scales poorly suited for back calculation.

A comparison of a validated otolith method to age weakfish, *Cynoscion regalis*, with the traditional scale method

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The weakfish, *Cynoscion regalis*, is a recreationally and commercially important sciaenid found from eastern Florida to Massachusetts, and is most abundant from North Carolina to New York (Mercer, 1985). Believed to be resident year-round in the Carolinas, they are found farther north only seasonally (Bigelow and Schroeder, 1953). In the spring, weakfish migrate northward and inshore to estuarine feeding and spawning grounds; this pattern is reversed in the fall (Wilk, 1979). Most fish are believed to overwinter off North Carolina (Pearson, 1932). Weakfish are found in Chesapeake Bay, roughly from April through November (Pearson, 1941; Massmann et al., 1958), where they support one of the region's most important fisheries (Rothschild et al., 1981).

Weakfish age and growth studies have been based almost exclusively on scales (Taylor, 1916; Nesbit, 1954; Perlmutter et al., 1956; Massmann, 1963a; Merriner, 1973; Shepherd and Grimes, 1983). However, problems with this method have been reported: 1) small fish may not lay down a first annulus on scales (Welsh and Breder, 1923), 2) older fish have closely spaced annuli that are difficult to interpret (Taylor, 1916; Shepherd, 1988), 3) annuli form over a long time period, April–August, and scales are difficult to interpret during annulus formation (Nesbit, 1954; Massmann, 1963b), 4) the time annuli form varies annually and regionally (Perlmutter et al., 1956), and 5) checks (false annuli) and regenerated scales are common (Merriner, 1973). The scale method of ageing weakfish also has not been conclusively validated by current standards (Beamish and McFarlane, 1983; Brothers, 1983). Perlmutter et al. (1956) and Shepherd and Grimes (1983) both tried to validate annuli on scales by the marginal increment method, however they used pooled age data and did not report the age range.

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Although recent studies have shown that for many species the scale method underages older fish at the point where fish growth becomes asymptotic (Beamish and Chilton, 1981; Beamish and McFarlane, 1983; Barnes and Power, 1984), there has been little evaluation of other weakfish hardparts. Merriner (1973) compared weakfish scales to whole vertebrae and otoliths, and Villoso (1989) compared scales to whole otoliths. Both concluded that scales were best. However, Merriner's study was conducted before thin-sectioning of otoliths (Williams and Bedford, 1974; Beamish, 1979; Beamish and Chilton, 1981) and other hardparts became common and Villoso (1989) did not consider thin-sectioning.

A decline in weakfish landings since 1980, coupled with greater competition between fisheries, caused the Atlantic States Marine Fisheries Commission (ASMFC) to develop a weakfish management plan in 1985 (Mercer, 1985). Since then the ASMFC has issued an updated stock assessment[1] and suggested a 25% reduction in coast-wide exploitation rates (Amendment No. 1 of the Weakfish Fishery Management Plan of the ASMFC). However, it is essential to proper weakfish management that a validated ageing technique be developed and used, as improper ageing can lead to faulty estimates of model parameters such as age at maturity, growth, longevity and mortality (Beamish and McFarlane, 1983).

The objectives of this study were 1) to compare otolith, dorsal-fin spine, and pectoral-fin ray sections with scales in terms of legibility and interpretation of potential annual marks, ease of collection and processing, and precision, 2) to validate the hardpart demonstrating the greatest clarity by marginal increment analysis for each age group found in the Chesapeake Bay area, and 3) to conduct a more in-depth comparison of the validated hardpart with scales in terms of precision and accuracy, time of annulus formation, growth estimates, and use in back calculation of body length.

Methods

Preliminary comparison of hardparts

Four hundred weakfish were collected every other week during April–October in 1989 from three Chesapeake Bay commercial pound nets. On each collection day, one 22.7 kg (50 lb) box of each available grade of weakfish—small, medium, or large—was bought and all fish within it processed. Fish were measured for total length (TL ±1.0 mm), sexed, and both sagittal otoliths were removed and stored dry. Scales were removed from an area just posterior to the tip of the left pectoral fin, below the lateral line. The left pectoral fin and the entire dorsal fin were removed by cutting below the base of the rays. Scales and fins were stored in paper envelopes and kept frozen until preparation for ageing.

A total of 45 fish, 15 from each grade, were randomly selected from the fish collected in 1989 for a preliminary comparison of hardparts. These fish ranged from 244 to 615 mm TL and each of their four hardparts was prepared for reading as described below.

The right otolith from each fish was transversely sectioned through the nucleus with a Buehler low-speed Isomet saw. Sections 350–500 µm thick were mounted on glass slides with Flo-Texx clear mounting medium and viewed under a dissecting microscope at 24× magnification by using transmitted light and bright field, with the exception of samples from the period April–May, when sections were also read with reflected light and dark field to help identify the last annulus. Thin opaque bands, presumed to represent annual marks, were counted along the otolith sulcal groove (Fig. 1). Because opaque bands inhibit light passage, they appeared dark in transmitted light (Fig. 2A) and light in reflected light.

Scales from each fish were soaked in water until soft, after which they were washed gently with a soft-bristled tooth brush. Three or four clean, unregenerated scales

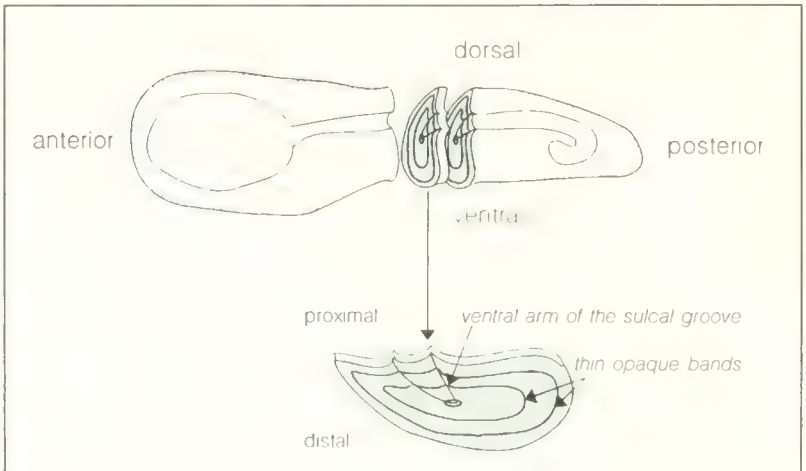

Figure 1

Schematic representation of a transverse section taken through the right sagittal otolith. The ventral arm of the sulcal groove, along which otoliths were measured, is indicated. The whole otolith is positioned as it would be in a weakfish, *Cynoscion regalis*.

[1] Vaughan, D. S., R. J. Seagraves, and K. West. 1991. An assessment of the Atlantic weakfish stock, 1982–1988. Atl. States Mar. Fish. Comm. Spec. Rep. 21, Wash. DC, 29 p.

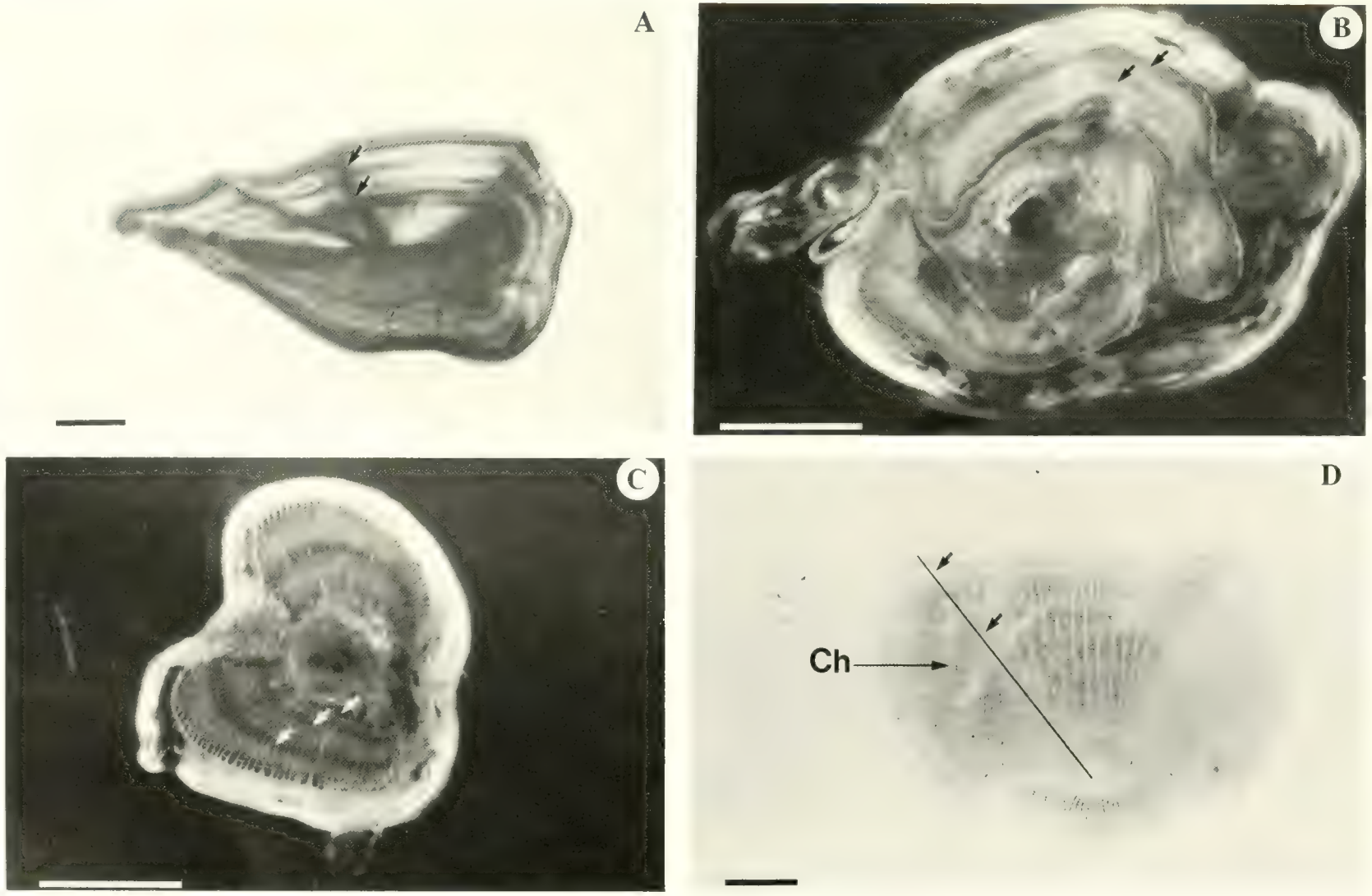

Figure 2

Marks on hardparts taken from a two-year-old (as aged by otoliths) female weakfish, *Cynoscion regalis*, TL=392 mm, collected in mid-September. (**A**) otolith section, as seen in transmitted light, bar=1 mm; (**B**) pectoral ray section, as seen in transmitted light and dark field, bar=0.5 mm; (**C**) dorsal spine section, as seen in transmitted light and dark field, bar=0.5 mm; and (**D**) scale impression, as seen in transmitted light, bar=1 mm. The left radius, which was the scale measuring axis, is marked. Ch=check. Arrows indicate individual marks counted.

were then dried, taped to an acetate sheet, inserted between two other blank sheets, and pressed with a Carver laboratory scale press for two minutes at 2,721 kg of pressure at 71°F. Because of the large size of weakfish scales, scale impressions were read with a standard microfiche reader at 20×. Those scales with potential annuli crowded along the scale periphery were also viewed at 48× under a dissecting microscope. Presumed annual marks were identified by standard criteria (Bagenal and Tesch, 1978; Shepherd, 1988).

One spiny ray from the dorsal fin and one soft ray of the left pectoral fin were prepared from each fish. Rays were serially sectioned by starting at their base and cutting through most of their length at a thickness of 400 µm with a Buehler low-speed Isomet saw. Sections were then mounted on microscope slides with Flo-Texx and read under a dissecting microscope with transmitted light and dark field at 64×. Presumed annual marks were counted when they could be identified as individual, opaque bands.

Each hardpart was read twice by two separate readers. Readings were done in a randomly selected order, with no knowledge of collection date or fish size. Hardparts were evaluated in terms of clarity of presumed annual marks, ease of collection and processing, and precision. Precision was measured by average percent agreement within and between readers, i.e. percent agreement within readers was calculated for each reader separately and then averaged for the two readers and percent agreement between readers was calculated separately for each reading and then averaged for the two readings.

Validation of the otolith method

Because otoliths were found best for ageing, additional samples were collected for validation. During 1989–92, 1,928 weakfish were collected from commercial pound-net, haul-seine, and gill-net fisheries in Chesapeake Bay. During March–November when weakfish are not present in the Chesapeake Bay, fish were collected (n=289) from the trawl fishery operating in North Carolina shelf waters north of Cape Hatteras.

The marginal increment method was used to validate otolith annuli (Brothers, 1983; Casselman, 1987; Hyndes et al., 1992). The translucent margin outside the proximal end of the last annulus was measured along the ventral side of the otolith sulcal groove (Fig. 1). Measurements were taken with an ocular micrometer to the nearest 0.038 mm (one micrometer unit at a total magnification of 24×).

Comparison of scales and otoliths

To compare the otolith and scale methods in more detail, 155 fish ranging from 140 to 845 mm TL were selected by stratified, random subsampling—strata being otolith-determined ages—from a total of 300 fish collected in 1989 and 1992. Thirty fish were selected from each of the age-strata, 1–4. Because older fish were scarce, only 14 age-5, 16 age-6, two age-7, two age-8, and one age-10 fish were included. Although most fish came from Chesapeake Bay commercial fisheries, in order to increase the number of older fish, 27 fish were collected in May 1992 at the Delaware Bay Weakfish Sport Fishing Tournament. We collected an additional 20 fish in August 1992 to include fish from each of the summer months for marginal increment and back-calculation analyses.

Hardparts were prepared as described for the preliminary comparison and read twice by each of two readers. An effort was made to determine annuli on scales based only on physical criteria and not to assign annuli based on any preconceived ideas of growth (Casselman, 1983). Reading order was randomized and collection date and fish size were unknown. Each reader recorded the number of presumed annuli and a "+" if there was growth beyond the last annulus or a "*" if the last presumed annulus was forming or had just formed (Casselman, 1987). After all hardparts had been read, we assigned ages using a January 1 birthdate, knowledge of the time of annulus formation, the relative growth of the hardpart margin, and date of capture.

Variability within reader, between readers, and between hardparts was analyzed by percent agreement. When an individual reader's counts of presumed annuli disagreed, a third reading was made. When readers' ages disagreed, a third reading with both readers present was made to resolve the disagreement.

To compare time of annulus formation and its variability in scales and otoliths, mean monthly relative marginal increments and their ranges were calculated and plotted (April–October). Relative marginal increments were calculated by dividing the marginal increment by the hardpart radius. All ages were pooled. Additionally, those hardparts which had been designated as having an annulus on the margin ("*") were reviewed and their time of collection recorded.

To determine marginal increments and to conduct back-calculation analyses, hardparts were measured by using a Via 100 camera/monitor system with a dissecting microscope at 24×. Otolith radius (OR) and otolith annular radius (OAR)—the distance from the nucleus to the proximal edge of each annulus—were measured along the ventral arm of the sulcal groove. Scale radius (SR) and scale annular radius (SAR) were measured along the left radius (Ricker, 1992). Marginal growth was measured from outside the last annulus to the hardpart edge.

To evaluate the applicability of scales and otoliths for back-calculation, it was necessary to first analyze separately their total length to hardpart relationships. Seasonal effects were assessed by comparing hardpart size of one age class taken from different seasons to that predicted by the linear regression of total length on hardpart size for all fish. Only one age class (age 3) was used to remove any confounding effects of age. This age class was chosen because it was well-represented throughout the seasons.

Back-calculation relationships for both scales and otoliths were based on the "body proportional" hypothesis (Francis, 1990) proposed by Whitney and Carlander (1956):

$$L_i = [g(S_i) / g(S_c)] L_c,$$

where g is the total length on hardpart radius function, L_i is back-calculated TL at age i, S_i is the measured hardpart size at annulus i, and S_c and L_c are the respective hardpart size and total length at capture. Only fish collected in April and May—the beginning of the somatic growth season—were used, to remove seasonal effects from the back-calculation equations (Ricker, 1992). Because body-proportional back-calculation is based not just on the relationship of hardpart size to total length but also on the relationship of hardpart size to consecutive annuli, mean annual growth increments were also calculated and compared between scales and otoliths.

The tendency for older fish to produce smaller back-calculated lengths at younger ages than observed, known as Lee's phenomenon (Smith, 1983), was evaluated by calculating mean SAR and mean OAR for each age at capture. In this way it was possible to determine if older fish demonstrated slower hardpart growth at younger ages, i.e. true Lee's phenomenon (Smale and Taylor, 1987).

Data were analyzed by using χ^2 tests and regression methods available through the Statistical Analysis System (SAS 1988). Rejection of the null hypothesis in statistical tests was based on α=0.05. Assumptions of linear models were checked by residual plots as described in Draper and Smith (1981).

Results

Preliminary comparison of hardparts

All four hardparts showed concentric marks that were interpreted as annuli (Fig. 2). However, marks on the dorsal spines and pectoral rays were inconsistent, often blurred or impossible to follow around most of the section and therefore difficult to interpret. Presumed annuli on scales were distinctly clearer and more regular than those on dorsal spines and pectoral rays, but they still required some subjective interpretation. Presumed annuli on otoliths were exceptionally clear, consistent, and easy to interpret.

Typical otolith sections showed an opaque nucleus surrounded by a translucent zone followed by a pattern of thin, opaque zones alternating with wide, translucent zones along the sulcal groove (Fig. 2A). In some sections the translucent zone between the nucleus and the first opaque zone was relatively small and made more opaque by a number of fine, circular, opaque bands. However, in all sections the first opaque zone beyond the nucleus was easily identified and considered to be the first annulus.

Presumed annuli on scales were harder to identify than those on otoliths but were usually identifiable as a clear zone in the anterior field, where circuli are either absent or more widely spaced, and by cutting over in the lateral fields (Fig. 2D). Checks were most apparent in the anterior field. A clear zone in the anterior field was considered a check if it was not accompanied by distinct cutting over in the lateral fields. The first annulus was the hardest to identify. It rarely showed a clear band in the radii zone, although cutting over was sometimes apparent. Its position was based predominantly on the first point at which a large number of secondary radii originated.

Presumed annual marks on dorsal spines were fairly clear in some sections but incomplete or blurred in others (Fig. 2C), whereas pectoral-fin ray sections were consistently hard to interpret (Fig. 2B). Presumed annual marks on both these hardparts appeared as wide, opaque, semicircular bands alternating with narrow translucent zones.

Otoliths showed the greatest precision, with 100% average agreement within and between readers. Scales also had high average agreement: 89% within readers and 80% between readers. Dorsal and pectoral fin sections showed the lowest agreement (Table 1) and little confidence was attached to their age assignments.

Table 1

Average percent agreement in the preliminary comparison of weakfish, *Cynscion regalis*, hardpart mark counts within readers, between readers, and with otoliths.

Hardpart	Within readers	Between readers	With otoliths
Scales	89	80	27
Pectoral rays	59	64	49
Dorsal spines	66	76	46
Otoliths	100	100	

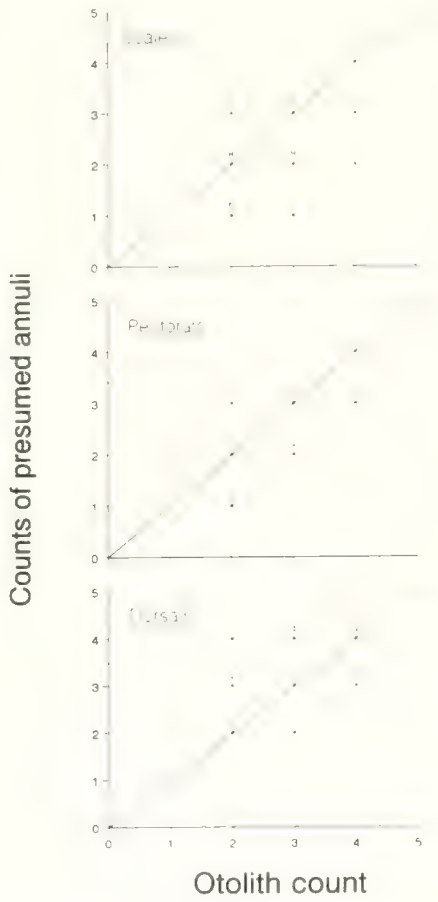

Figure 3

Counts of presumed annuli from weakfish, *Cynoscion regalis*, scales, pectorals, and dorsals compared with otoliths. The number of fish each point represents is indicated. The 45° line represents 100% agreement.

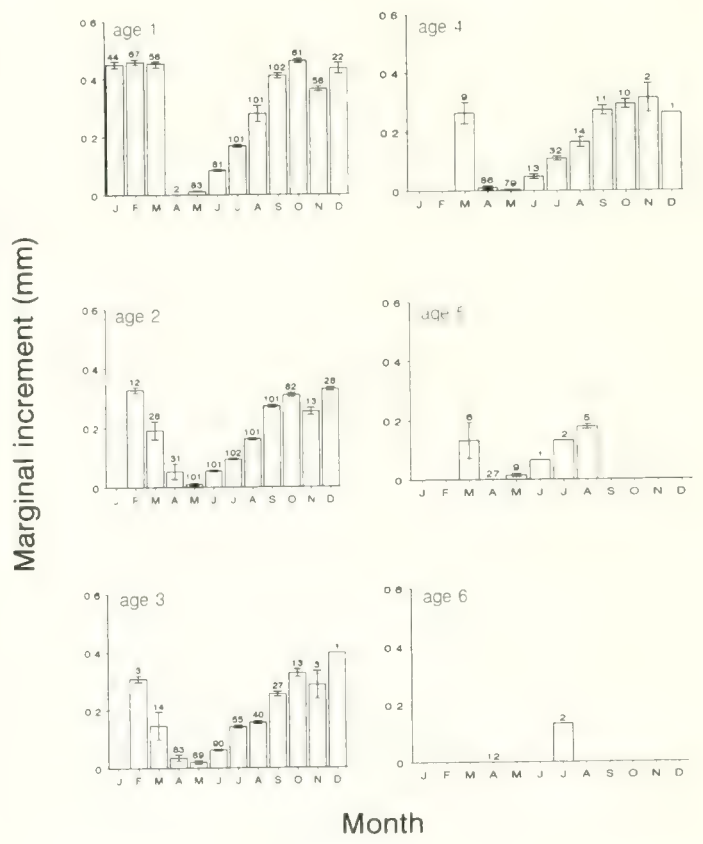

Figure 4

Mean monthly otolith marginal increments for weakfish, *Cynoscion regalis*, ages 1–6 from the Chesapeake Bay region, 1989–91. Vertical bars are ± one standard error. Numbers above the bars represent sample size.

The number of presumed annual marks on otolith sections agreed poorly with those on other hardparts (Fig. 3). Scale and otolith readings agreed only 27% of the time (Table 1) and scales consistently had one less mark than otoliths (26 out of 45). Pectoral and dorsal rays showed better agreement with otoliths than with scales, 49% and 46% respectively.

Validation of the otolith method

Opaque bands are laid down on otoliths once a year in the spring. Mean monthly marginal increment plots for ages 1–6 showed only one trough during the year, indicating only one opaque band was formed per year (Fig. 4). A few fish began to lay down annuli in March, as shown by the decrease in mean marginal increment and a relatively high variation in marginal increment size. However, lowest marginal increment values occurred in April and May, indicating most fish formed annuli during these months. Greatest otolith growth occurred during the months of June, July, August, and September, as demonstrated by the step-wise increase in mean marginal increments. By October, mean marginal increments reached a fairly stable maximum, indicating little or no otolith growth. This maximum continued until the next March or April, when annuli were again laid down.

Because of the scarcity of older fish, it was not possible to validate conclusively fish older than age 5 by separate marginal increment plots. However, there was no evidence that the pattern of annulus formation changed within the weakfish lifespan. Annuli were consistently formed during March–May for fish of different sizes, sexes, and ages (1–6), and otoliths did not form more than one mark per year even though these ages represented various stages in the

fish's life history. Additionally, of the 2,217 otoliths examined (ages 1–10), all those in the process of forming or which had just formed annuli were collected in March–May. Thus, we assumed for ages 1–10 that the otolith method provided accurate ages.

Comparison of scales and otoliths

Scales were consistently more difficult to read than otoliths, and confidence in scale readings was often low. Percent agreement within and between readers was fairly consistent for both hardparts. However, otoliths showed much higher agreement (98–100%), than did scales (78–80%) (Table 2). Although agreement between scales and otoliths was fairly high, 79%, agreement decreased with increasing age. Of 32 disagreements, only 6 differed by more than one year (Fig. 5). However, 4 of the 5 fish older than age 6 were underaged by scales and two of the oldest fish, age 10 and 8, were underaged by 3 years. Scales from older fish, if they showed more than 6 annuli, had marks which were severely crowded and fragmented even when viewed at higher magnification (Fig. 6A), whereas otoliths from these same fish showed clear annuli (Fig. 6B).

Although the number of fish underaged was small, their effect on estimating growth curves would be dramatic. Mean body size at age based on scales, although slightly curvilinear, showed no clear indication of an asymptote (Fig. 7A) and thus would not be appropriate for fitting a von Bertalanffy growth curve (Gallucci and Quinn, 1979). In contrast, mean body size at age based on otoliths showed the clear beginnings of an asymptote (Fig. 7B).

Although sex of the fish had no effect on the precision or repeatability of scale readings, it did affect accuracy. Agreement of scale ages among and between readers was quite similar when calculated separately by sex, ranging from 75 to 79.5%. However, agreement between scale and otolith ages, or accuracy, was significantly different for males and females (χ^2=6.25, n=154, P<0.05). Of the 32 discrepancies between scale and otolith ages, 26 of them were males. Even if the fish greater than age 6 are discounted, there is still a significant difference (χ^2=5.79, n=149, P<0.05).

Time of annulus formation is not the same for scales and otoliths. Both hardparts showed only one trough in their mean monthly marginal increments (Fig. 8). However, otoliths with annuli on their margins were collected only during a discrete time period, 1 April–1 June, while scales in the process of forming annuli were collected from mid-April to mid-August, although most scales formed annuli in August. The variable and extended time of scale annulus formation is represented by the shallow trough (Brothers, 1983) and the larger standard errors of the scale marginal increment plot, as compared with that of otoliths (Fig. 8).

Although total length on hardpart size relationships for both scales and otoliths showed linear trends (r^2=0.94 and 0.88 respectively, n=175, P=0.0001), the total length on otolith relationship showed seasonal variation. When a single age class (age 3) was marked by season of collection and plotted against the linear relationship predicted by the total sample (Fig. 9), all fish collected in April and May had smaller than predicted otolith radii, whereas fish collected in August and September had larger than predicted radii. Fish collected in June and July were intermediate, although most of their radii were also smaller than predicted. Scales from the same fish did not show similar seasonal trends.

Back-calculation equations of total length on hardpart size were calculated only for fish collected at the beginning of the growing season, in April and

Table 2

Percent agreement of weakfish, *Cynoscion regalis*, scale- and otolith-assigned ages within readers, between readers, and between hardparts.

Hardpart	Within reader 1	Within reader 2	Between readers	With otoliths
Scales	80	78	80	79
Otoliths	100	98	99	

Figure 5

Weakfish, *Cynoscion regalis*, assigned ages from scales and otoliths. The number of fish each point represents is indicated. The 45° line represents 100% agreement.

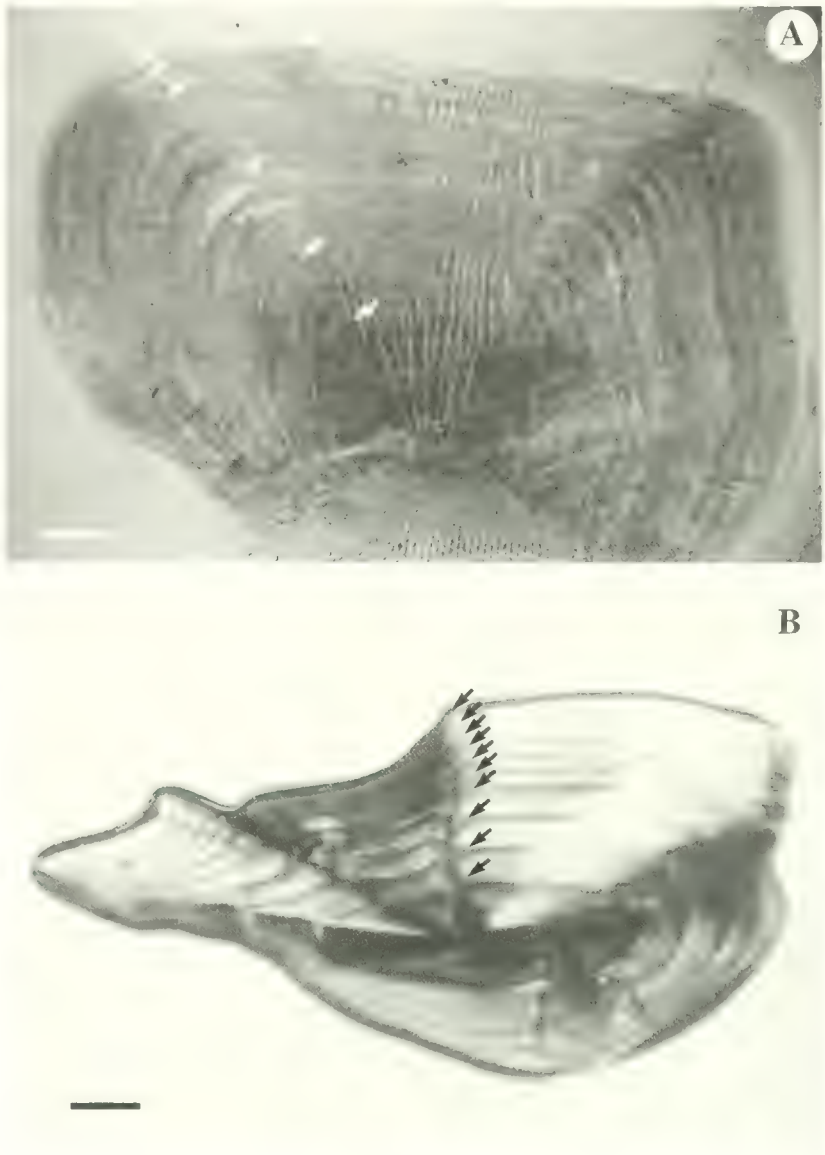

Figure 6

The scale impression (**A**) and sectioned otolith (**B**), as seen in transmitted light, from a male, 10-year-old weakfish, *Cynoscion regalis*, TL=845 mm, collected in mid-May. Arrows indicate marks counted as annuli.

May, to remove seasonal effects. Although linear regressions were significant for scales (r^2=0.95, P=0.0001) and otoliths (r^2=0.92, P=0.0001), a quadratic term improved the model fit and was significant (P=0.0003 scales, P=0.0001 otoliths) (Fig. 10). Equations were

For scales:

$$TL = -151.6 + 160.2\ SR - 5.4\ SR^2\ (r^2=0.96, n=88, P=0.0001);$$

For otoliths:

$$TL = -220.9 + 543.1\ OR - 66.9\ OR^2\ (r^2=0.94, n=88, P=0.0001).$$

The pattern of mean annual growth increments differed between scales and otoliths. Both scales and otoliths showed their largest growth increment from the focus to the first annulus (Fig. 11). However, once fish had reached age 1, the largest otolith annual growth increment occurred between the first and

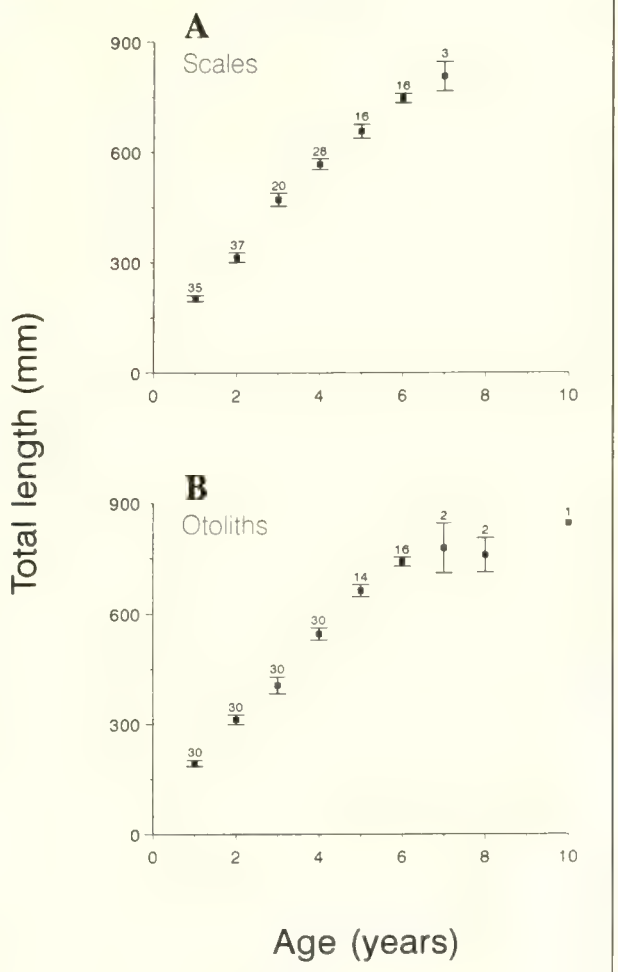

Figure 7

Mean weakfish, *Cynoscion regalis*, size at age: (**A**) based on scales and (**B**) based on otoliths. Vertical bars are ± one standard error. Numbers above the bars represent sample size.

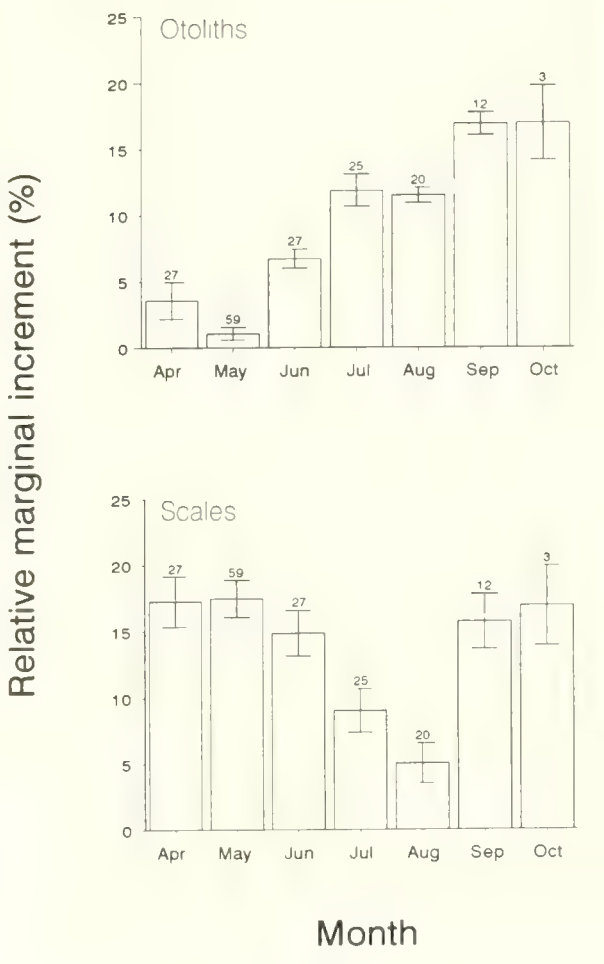

Figure 8

Mean monthly relative increments for weakfish, *Cynoscion regalis*, scales and otoliths. Vertical bars are ± one standard error. Numbers above the bars represent sample sizes.

second annuli, whereas scales had a very small increment between these annuli. The largest scale growth increment after age 1 was between annuli 3 and 4. Neither hardpart showed a consistently decreasing mean annual growth increment as age increased. Although this assumption is often included in scale-reading criteria, it would be inappropriate for weakfish.

Back-calculated mean body sizes at age were larger for scales than for otoliths (Table 3). In part, this discrepancy may reflect different times of annulus formation: back-calculated lengths from scales, in general, estimate sizes in August, whereas back-calculated lengths from otoliths estimate sizes in April and May. Also, at older ages, back-calculated body sizes at age based on scales would be expected to be larger because of the underageing of older fish by scales.

Both scales and otoliths showed smaller back-calculated mean body size at age 1 than observed. At later ages, back-calculated TL's from scales were larger than observed, while back-calculated TL's from otoliths showed no consistent trend (Table 3). The cause of the smaller back-calculated TL's at age 1, however, did not appear related to Lee's phenomenon, as there was no consistent trend of smaller age-1 annular radii at older ages at capture (Tables 4 and 5). In fact, the largest mean SAR and OAR at age 1 came from 5-year-old fish. However, age-1 OAR's from the oldest fish in the study (>age 6, n=5) were distinctly smaller than those observed in younger fish.

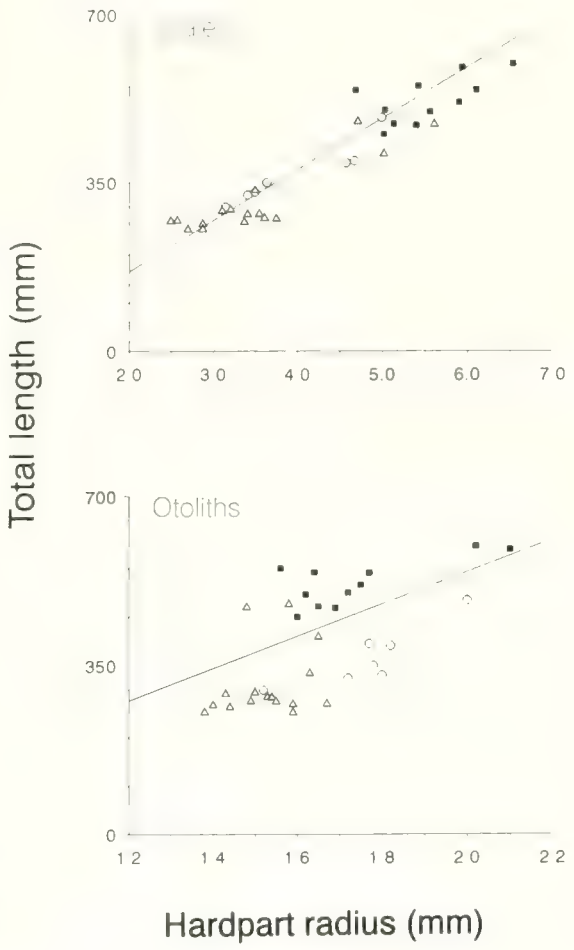

Figure 9

Total length plotted on hardpart size for age-3 weakfish, *Cynoscion regalis*, n=35. Lines represent the linear total length to hardpart regressions calculated from all fish, n=175. Fish are marked by season of collection: open circles=April–May; shaded triangles=June–July; and black squares=August–September.

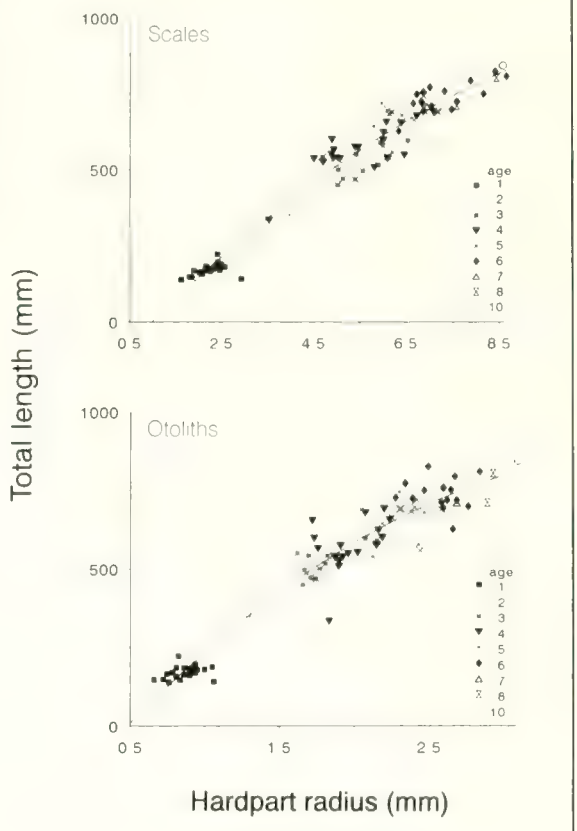

Figure 10

Weakfish, *Cynoscion regalis*, total length on hardpart radius regression used for back calculation. Based on fish collected in April and May, n=88.

Discussion

Our results indicate that transverse otolith sections are the best method to age weakfish. Sectioned otoliths were characterized by thin opaque bands, considered annuli, interspersed with wider translucent zones. This pattern is similar to other sciaenids, such as spotted seatrout, *Cynoscion nebulosus* (Maceina et al., 1987), Atlantic croaker, *Micropogonias undulatus* (Barbieri et al., 1994), red drum, *Sciaenops ocellatus* (Murphy and Taylor, 1991), and black drum, *Pogonias cromis* (Beckman et al., 1990). This pattern should not be confused with the more

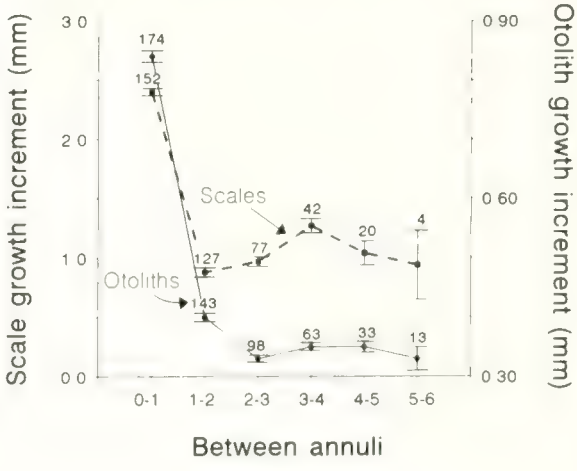

Figure 11

Mean annual growth increments of weakfish, *Cynoscion regalis*, scales and otoliths. Vertical bars are ± one standard error. Numbers above the bars represent sample sizes.

common otolith pattern found in many temperate fish of thin translucent zones, which are considered annuli, interspersed with wide opaque zones (Hyndes et al., 1992).

Table 3

Mean back-calculated weakfish, *Cynoscion regalis*, total lengths (mm) at age based on scales and otoliths, calculated from a quadratic body to hardpart regression and observed mean total length at time of annulus formation. Sample size is in parentheses.

Age	Scales	Observed Jul/Aug	Otoliths	Observed April/May
1	196 (152)	240 (7)	162 (174)	172 (22)
2	305 (127)	296 (25)	297 (144)	260 (2)
3	422 (77)	377 (8)	421 (99)	532 (12)
4	564 (42)	514 (5)	552 (64)	566 (18)
5	682 (20)		660 (34)	663 (14)
6	733 (4)		711 (14)	741 (16)
7			750 (5)	710 (1)
8			748 (2)	759 (2)
10				845 (1)

Table 4

Mean scale annular radii (SAR) for each scale age of weakfish, *Cynoscion regalis*.

		Scale annulus					
Age	*n*	1	2	3	4	5	6
1	12	2.59					
2	52	2.31	3.20				
3	24	2.40	3.42	4.14			
4	29	2.38	3.27	4.27	5.56		
5	16	2.65	3.44	4.31	5.43	7.15	
6	16	2.38	3.25	4.30	5.58	6.64	7.00
7	3	2.11	3.09	3.92	5.65	6.69	7.37

Table 5

Mean otolith annular radii (OAR) for each otolith age of weakfish, *Cynoscion regalis*.

		Otolith annulus							
Age	*n*	1	2	3	4	5	6	7	8
1	29	0.83							
2	45	0.85	1.27						
3	35	0.82	1.21	1.56					
4	30	0.82	1.20	1.53	1.91				
5	14	0.88	1.25	1.58	1.91	2.28			
6	16	0.86	1.22	1.54	1.88	2.21	2.52		
7	2	0.80	1.18	1.47	1.79	2.16	2.47	2.79	
8	2	0.77	1.20	1.56	1.90	2.22	2.47	2.65	2.85
10	1	0.67	1.11	1.52	1.94	2.15	2.32	2.49	2.67

Sectioned otoliths were consistently clear and easy to read, as shown by the high precision of repeated age readings. Although it was possible only to validate ages 1–5 by separate marginal increment plots, otolith annuli in all ages examined (1–10) were laid down once a year during a discrete time period (April–May). The constancy of annulus deposition at older ages, the lack of severely crowded annuli in older fish, and the similarity between weakfish otoliths and other sciaenid otoliths that have been validated at older ages (Beckman et al., 1990, Murphy and Taylor, 1991; Barbieri et al., 1994) suggest that otoliths are a reliable ageing technique for weakfish, although older ages must still be validated.

In contrast, we found the scale method of ageing weakfish to be imprecise and apparently inaccurate at older ages. We found that scales form annuli over an extended period, April–August, similar to the results of past studies (Perlmutter et al., 1956; Massmann, 1963b). This protracted period of annulus formation made it difficult to assign ages to fish taken in midsummer with moderate growth on the scale margin, as noted by Massmann (1963b). For example, a fish taken in July with a medium marginal increment on its scale could have formed its annuli in early April and have grown since then, or it could have increased its growth increment before forming an annulus in August. Thus, assigning an age to these fish is purely subjective and can lead to ageing errors ± one year, which may explain most of the discrepancies between otolith and scale ages.

The long period of annulus formation on scales and the severe crowding of annuli at older ages make it difficult to validate scales by the marginal increment method—as Perlmutter et al. (1956) and Shepherd and Grimes (1983) attempted for pooled age data. Because scale annuli form over a protracted period, the trough in the marginal increment plot is shallow and the range of marginal growth during other months is large. Additionally, validation by the marginal increment method is not appropriate if the hardpart shows severe crowding of annuli at older ages, as we found with scales, and has been previously reported (Shepherd, 1988). Shepherd (1988) described annuli in fish older than age 6 or 7 as being crowded and very difficult to detect, which could lead to marginal increments being measured from the last distinguishable annulus to the edge, rather than from the last real annulus to the edge. This error would inflate marginal increment estimates and there would be no way to detect underaged, older fish in marginal increment plots.

The scale method appears to underage older weakfish. Assuming otolith ages were valid, 4 of the 5 fish in this study older than age 6 were underaged by scales. Although 4 out of 155 fish may seem insignificant, the importance of correctly ageing these fish cannot be judged only by the number of discrepancies. These fish represent the beginning of an asymptote in growth and fish in the asymptotic range are often rare in highly exploited stocks. Obtaining and correctly ageing a few weakfish in this range is critical to correctly estimating the parameters of the von Bertalanffy growth curve.

Annulus formation on weakfish otoliths and scales shows different patterns. The formation of otolith annuli over a discrete time period suggests it may be caused by environmental variables. The most commonly suggested environmental influences on annulus formation are temperature, salinity, food, and light (Simkiss, 1974). Weakfish form annuli on their otoliths in April and May, when they migrate from offshore winter grounds to estuarine feeding and spawning grounds. Thus, annulus formation may be linked to their migration into a different environment.

Weakfish scales, in contrast, have a more variable time of annulus formation suggesting a cause other than general environmental conditions. Scales may undergo resorption whereas otoliths do not (Simkiss, 1974), and spawning has been linked to scale resorption with a consequent scale mark in salmon and trout (Crichton, 1935). Spawning may also be linked to formation of annuli on weakfish scales (Merriner, 1973). Weakfish mature at age 1 (Merriner, 1976; Shepherd and Grimes, 1984) and are multiple spawners with a protracted spawning period from May through August (Lowerre-Barbieri[2]). However, individual spawning periods are asynchronous and vary greatly, especially in time of termination. Spawning activity and annulus formation may be linked in two ways: 1) annuli could form on scales early in the spawning season when resources are shifted towards production of reproductive materials—especially the yolking of oocytes, or 2) annuli might form near the end of the season, owing to the cumulative drain of protracted spawning, causing a cessation in growth and thus an annulus. A connection between scale annulus formation and spawning in weakfish would explain the high level of variation in time of annulus formation and the higher accuracy of ages based on scales taken from females, because females usually invest more energy in reproduction. It might also explain the small growth increment between annuli 1 and 2 if one-year-old weakfish begin spawning later in the season than older fish, owing to a threshold size necessary to reach maturity.

Our results indicate both scales and otoliths present problems for back-calculation of weakfish. Although scales showed a strong relationship between body and hardpart size and no seasonal differences in growth, their long and variable time of annulus formation may cause considerable error (Smith, 1983). It is impossible to determine if a fish formed its annuli at the same time each year. Because annuli can form from April to August, increments may represent 8–16 months of growth rather than approximately one year of growth. Additionally, scale annuli are more difficult to distinguish than otolith annuli, making SAR's difficult to measure and somewhat subjective. However, otoliths show seasonal change in the body to hardpart relationship, making a season-specific back-calculation equation, such as we developed, inappropriate for fish collected outside of that season. Additionally, comparisons between back-calculated and observed sizes at age were complicated by the weakfish migrational pattern, since weakfish age ranges in the Chesapeake Bay vary seasonally—older fish are present only in spring and only occasionally in fall (Joseph, 1972).

There was no clear evidence of Lee's phenomenon, as older fish did not consistently show smaller hardpart size at younger ages. The five oldest fish did, however, demonstrate considerably smaller OAR's at age 1 than did their younger counterparts. Nevertheless, these same fish did not demonstrate consistently smaller OAR's at consecutive ages than did younger fish. Thus, the smaller OAR's at age 1, rather than demonstrating Lee's phenomenon, may simply reflect when most fish of those year classes were born, i.e. fish born early in the spawning season would have larger OAR's at age 1 because they had more time to grow before winter, than did fish born later in the season.

Previous criticism of back-calculation has focused mainly on the body size to hardpart relationship and its calculation (Campana, 1990; Casselman, 1990; Francis, 1990; Ricker, 1992). However, the validity of back-calculation also depends on the constancy, clarity, and pattern of hardpart growth increments. The different growth increment patterns we found between scales and otoliths demonstrate the need to understand hardpart growth better, how it relates to somatic growth and what causes annulus formation on different hardparts.

Future studies of weakfish age and growth should be based on sectioned otoliths because scales appear inaccurate once growth becomes asymptotic. This common failing of the scale method has been reported for many species (Beamish and McFarlane, 1987). It

[2] Lowerre-Barbieri, S. K. 1993. Reproductive biology of weakfish, *Cynoscion regalis*, in the Chesapeake Bay region. School of Marine Science, VIMS, College of William and Mary, unpubl. manuscr.

can result in underestimates of longevity, overestimates of mortality, inaccurate growth calculations, and improper modelling and management decisions (Beamish and McFarlane, 1983). Similarly, current estimates of weakfish growth, longevity, and mortality may need to be reevaluated, as suggested by our findings that scales underage older fish and have crowded annuli past age 6. The need for this reevaluation is underscored by the recording of a 17-year-old, as aged by otoliths, which was previously aged as a 7-year-old by scales (Lowerre-Barbieri[3]).

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Literature cited

Bagenal, T. B., and F. W. Tesch.
1978. Age and growth. *In* T. B. Bagenal (ed.), Methods for assessment of fish production in fresh waters, 3rd ed., p. 101–136. Blackwell Scientific Publs., Oxford.

Barbieri, L. R., M. E. Chittenden Jr., and C. M. Jones.
1994. Age, growth, and mortality of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay region, with a discussion of apparent geographic changes in population dynamics. Fish. Bull. 92:1–12.

Barnes, M. A., and G. Power.
1984. A comparison of otolith and scale ages for western Labrador lake whitefish (*Coregonus clupeaformis*). Env. Biol. Fish. 10:297–299.

Beamish, R. J.
1979. Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. J. Fish. Res. Board Can. 36:141–151.

Beamish, R. J., and D. E. Chilton.
1981. Preliminary evaluation of a method to determine the age of sablefish (*Anoplopoma fimbria*). Can. J. Fish. Aquat. Sci. 39:277–287.

Beamish, R. J., and G. A. McFarlane.
1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735–743.
1987. Current trends in age determination methodology. *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 15–42. Iowa State Univ. Press, Ames.

Beckman, D. W., A. L. Stanley, J. H. Render, and C. A. Wilson.
1990. Age and growth of black drum in Louisiana waters of the Gulf of Mexico. Trans. Am. Fish. Soc. 119:537–544.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv. Fish Bull. 53:1–577.

Brothers, E. B.
1983. Summary of round table discussions on age validation. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:35–44.

Campana, S. E.
1990. How reliable are growth back-calculations based on otoliths? Can. J. Fish. Aquat. Sci. 47:2219–2227.

Casselman, J. M.
1983. Age and growth assessment of fish from their calcified structures—techniques and tools. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:1–17.
1987. Determination of age and growth. *In* A. H. Weatherley and H. S. Gill (eds.), The biology of fish growth, p. 209–242. Academic Press, London.
1990. Growth and relative size of calcified structures of fish. Trans. Am. Fish. Soc. 119:673–688.

Crichton, M. I.
1935. Scale resorption in salmon and sea trout. Salm. Fish., Edinb. 4:1–8.

Draper, N. R., and H. Smith.
1981. Applied regression analysis, 2nd ed. John Wiley & Sons, New York, 709 p.

Francis, R. I. C. C.
1990. Back-calculation of fish length: a critical review. J. Fish Biol. 36:883–902.

Gallucci, V. F., and T. J. Quinn II.
1979. Reparameterizing, fitting, and testing a simple growth model. Trans. Am. Fish. Soc. 108:14–25.

Hyndes, G. A., N. R. Loneragan, and I. C. Potter.
1992. Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead, *Platycephalus speculator*. Fish. Bull. 90:276–284.

Joseph, E. B.
1972. The status of the sciaenid stocks of the middle Atlantic coast. Chesapeake Sci. 13:87–100.

[3] Lowerre-Barbieri, S. K. 1993. Age and growth of weakfish, *Cynoscion regalis*, in the Chesapeake Bay region. School of Marine Science, VIMS, College of William and Mary, unpubl. manuscr.

Maceina, M. J., D. N. Hata, T. L. Linton, and A. M. Landry Jr.
1987. Age and growth analysis of spotted seatrout from Galveston Bay, Texas. Trans. Am. Fish. Soc. 116:54–59.

Massmann, W. H.
1963a. Age and size composition of weakfish, *Cynoscion regalis*, from pound nets in Chesapeake Bay, Virginia, 1954–1958. Chesapeake Sci. 4:43–51.
1963b. Annulus formation on the scales of weakfish, *Cynoscion regalis*, of Chesapeake Bay. Chesapeake Sci. 4:54–56.

Massmann, W. H., J. P. Whitcomb, and A. L. Pacheco.
1958. Distribution and abundance of gray weakfish in the York River system, Virginia. Trans. N. Am. Wildl. Conf. 23:361–369.

Mercer, L. P.
1985. Fishery management plan for the weakfish (*Cynoscion regalis*) fishery. North Carolina Dep. Nat. Res. Comm. Dev., Div. Mar. Fish., Spec. Sci. Rep. 46, 129 p.

Merriner, J. V.
1973. Assessment of the weakfish resource, a suggested management plan, and aspects of life history in North Carolina. Ph.D. diss., North Carolina State Univ., Raleigh, NC, 201 p.
1976. Aspects of the reproductive biology of the weakfish, *Cynoscion regalis* (Sciaenidae), in North Carolina. Fish Bull. 74:18–26.

Murphy, M. D., and R. G. Taylor.
1991. Direct validation of ages determined for adult red drums from otolith sections. Trans. Am. Fish. Soc. 120:267–269.

Nesbit, R. A.
1954. Weakfish migration in relation to its conservation. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. Fish. 115, 81 p.

Pearson, J. C.
1932. Winter trawl fishery off the Virginia and North Carolina coasts. U.S. Bur. Fish. Invest. Rep. 10, 31 p.
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout *Cynoscion regalis* (Bloch and Schneider). U.S. Fish Wildl. Serv. Fish Bull. 50:79–102.

Perlmutter, A., W. S. Miller, and J. C. Poole.
1956. The weakfish (*Cynoscion regalis*) in New York waters. N.Y. Fish Game J. 3:1–43.

Ricker, W. E.
1992. Back-calculation of fish lengths based on proportionality between scale and length increments. Can. J. Fish. Aquat. Sci. 49:1018–1026.

Rothschild, B. J., P. W. Jones, and J. S. Wilson.
1981. Trends in Chesapeake Bay fisheries. Trans. N. Am. Wildl. Conf. 46:284–298.

SAS.
1988. SAS/STAT User's Guide, Release 6.03 ed. SAS Institute Inc., Cary, NC, 1029 p.

Shepherd, G. R.
1988. Age determination methods for northwest Atlantic species, weakfish *Cynoscion regalis*. *In* J. Penttila and L. M. Derry (eds.), Age determination methods for northwest Atlantic species, p.71–76. NOAA Tech. Rep. NMFS 72, 135 p.

Shepherd, G. R., and C. B. Grimes.
1983. Geographic and historic variations in growth of weakfish, *Cynoscion regalis*, in the Middle Atlantic Bight. Fish. Bull. 81:803–813.
1984. Reproduction of weakfish, *Cynoscion regalis*, in the New York bight and evidence for geographically specific life history characteristics. Fish. Bull. 82:501–511.

Simkiss, K.
1974. Calcium metabolism of fish in relation to ageing. *In* T. B. Bagenal (ed), The ageing of fish, p. 1–12. The Gresham Press, Old Woking, Surrey, England.

Smale, M. A., and W. W. Taylor.
1987. Sources of back-calculation error in estimating growth of lake whitefish. *In* R. C. Summerfelt and G.E. Hall (eds.), Age and growth of fish, p. 189–202. Iowa State Univ. Press, Ames.

Smith, C. L.
1983. Summary of round table discussions on back calculation. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8:45–47.

Taylor, H. F.
1916. The structure and growth of the scales of the squeteague and the pigfish as indicative of life history. Bull. U.S. Bur. Fish. 34:285–330.

Villoso, E. P.
1989. Reproductive biology and environmental control of spawning cycle of weakfish, *Cynoscion regalis* (Bloch and Schneider), in Delaware Bay. Ph.D. diss., Univ. Delaware, Newark, 295 p.

Welsh, W. W., and C. M. Breder Jr.
1923. Contributions to life histories of Sciaenidae of the eastern United States coast. Bull. U.S. Bur. Fish. 39:141–201.

Whitney, R. R., and K. D. Carlander
1956. Interpretation of body-scale regression for computing body length of fish. J. Wildl. Mgmt. 20(1):21–27.

Wilk, S. J.
1979. Biological and fisheries data on weakfish, *Cynoscion regalis* (Bloch and Schneider). U.S. Dep. Commer., NOAA, NMFS, NEFC, Sandy Hook Laboratory, Tech. Ser. Rep. No. 21, 49 p.

Williams, T., and B. C. Bedford.
1974. The use of otoliths for age determination. *In* T. B. Bagenal (ed), The ageing of fish, p. 114–123. The Gresham Press, Old Woking, Surrey, England.

Feeding habits of the dusky dolphin, *Lagenorhynchus obscurus*, in the coastal waters of central Peru

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Abstract.—In this study of the feeding habits of the dusky dolphin, *Lagenorhynchus obscurus*, stomach content samples were collected from dolphins caught by an artisanal fishery operating along the central coast of Peru. Collections were made from three fishing ports, Pucusana, Ancon, and Cerro Azul, during the summers and winters of 1985 and 1986. Overall, the anchoveta, *Engraulis ringens*, the most abundant vertebrate in Peruvian coastal waters, was the principal prey of dusky dolphins with respect to each of four different measures of dietary importance. Anchoveta was also the dominant prey in both seasons of both years, and for all reproductive classes of dusky dolphins. Other prey species commonly found in dolphin stomachs were horse mackerel, *Trachurus symmetricus*, hake, *Merluccius gayi*, sardine, *Sardinops sagax*, Patagonian squid, *Loligo gahi*, and jumbo flying squid, *Dosidicas gigas*. Regressions of body size on otolith or squid beak dimensions were used to estimate lengths and weights of anchoveta and some other prey. All prey species averaged less than 30 cm in estimated length and 300 g in weight. Estimated total lengths of anchoveta consumed as prey increased between seasons in 1985 and between years, paralleling the lengths of anchoveta taken by the purse-seine fishery. However, estimated total lengths of anchoveta eaten by dusky dolphins were consistently smaller than lengths of those caught by the fishery.

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The dusky dolphin, *Lagenorhynchus obscurus*, is common in the coastal waters of New Zealand, South America, and South Africa, but like most species of small cetacea from the Southern Hemisphere, its feeding habits are poorly described (Gaskin, 1982; Goodall and Galeazzi, 1985). The squid, *Nototodarus sloanei*, and fish have been reported as prey in New Zealand waters (Gaskin, 1972), whereas in Argentina Würsig and Würsig (1980) observed dusky dolphins feeding on southern anchovy, *Engraulis anchoita*. Prior to the present study, little was known of the feeding habits or natural history of the dusky dolphin in Peruvian waters, although large numbers of dusky dolphins were being taken in an artisanal fishery (Read et al., 1988; Van Waerebeek and Reyes, 1990).

In Peru, the dusky dolphin is found in the waters of the coastal upwelling system (McKinnon, 1988), which has been extensively studied by those involved in managing the system's various fisheries (Pauly and Tsukayama, 1987; Pauly et al., 1989). The cool waters of the coastal upwelling region constitute one of the most productive areas of the world ocean (Ryther, 1969), but oceanographic conditions and the abundance and distribution of fishes can vary greatly within and between years, especially when El Niño's occur (Pauly and Tsukayama, 1987; Pauly et al., 1989).

The objective of the present study was to characterize, in terms of both species composition and prey size, the feeding habits of the dusky dolphin in Peruvian waters. Seasonal and annual variation in feeding habits was also investigated and compared with abundance data for important prey species during the same periods. In addition, potential dietary differences among dolphins of different reproductive states were examined, as feeding habits of lactating females differ from those of nonlactating females and males in some small cetaceans (Bernard and Hohn, 1989; Recchia and Read, 1989).

Methods

Data on feeding habits were obtained by analysis of undigested hard parts of prey, specifically fish otoliths and squid beaks, from stomach content samples collected through the fishery. Dolphins were usually captured by artisanal fishermen in gill nets set from dusk to dawn within the coastal upwelling zone (Read et al., 1988; Van Waerebeek and Reyes, 1990), but six stomach samples from a single landing by a purse seiner, in the summer of 1985, were also included.

All samples were collected at ports along the central coast of Peru, where the largest dolphin catches occurred during the present

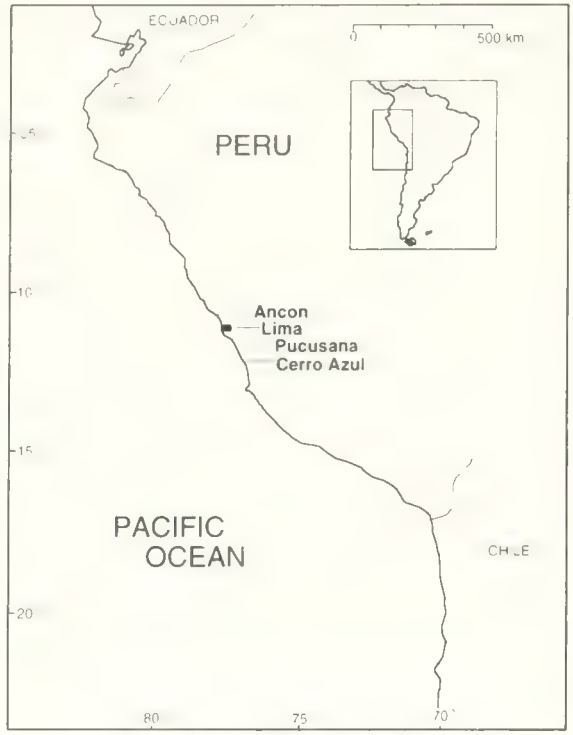

Figure 1

Map of Peruvian coastline, showing study sites. The inset shows the area in relation to the remainder of South America (Read et al., 1988).

study (Read et al., 1988). Pucusana, a small fishing town approximately 50 km south of Lima (Fig. 1) was the principal collecting site. Stomach content samples were also collected from the nearby ports of Cerro Azul and Ancon, about 70 km south and 90 km north of Pucusana, respectively (Fig. 1). Dolphin landings at any given port were highly variable (Read et al., 1988), therefore collecting efforts were concentrated at the port or ports where the most dolphins were being caught. The collecting periods were the austral summers (1 January through 31 March) and winters (1 July through 30 September) of 1985 and 1986.

Field procedures

Standard length, measured in a straight line along the main axis of the body from the tip of the upper jaw to the notch of the flukes, was taken for each specimen upon being landed. Females were pressed above the nipples and expression of milk, indicating lactation, was noted. When dolphins were eviscerated, female reproductive tracts were removed and checked for the presence of a fetus. Ovaries were inspected for corpora lutea and albicantia, then preserved in 10% formalin.

Collection of stomach contents also began upon evisceration, between approximately 6 and 48 hours after capture. Each of the fore-, main, and pyloric stomachs was separately rinsed through a series of three brass sieves (Treacy and Crawford, 1981; Murie and Lavigne, 1985) of mesh diameters 4.75, 1.40, and 0.425 mm. The sieved contents were then placed in deep, water-filled plastic trays so that any remaining flesh could be skimmed off. Fish otoliths and clean squid beaks were retrieved and stored in 5–10% alcohol; squid beaks with flesh still attached were stored in either 70% alcohol or 10% formalin. The forestomach consistently contained the least digested contents and the greatest volume, so only material from that chamber was later quantified and analyzed (see also Perrin et al., 1973; Bernard and Hohn, 1989).

Reproductive status

Reproductive status of females was classified after macroscopic examination of gonads and accessory reproductive tissues. Males were classified only as to sex. Females were defined as 1) immature, if their ovaries lacked corpora lutea and albicantia; 2) pregnant, if a fetus was visible in the uterus; 3) lactating; 4) simultaneously pregnant and lactating; or 5) resting, if corpora lutea or albicantia were present but there was neither a fetus visible in the uterus nor evidence of lactation (Perrin and Donovan, 1984). The "resting" category may have included females with small embryos not detected during field inspections, in addition to individuals actually between reproductive cycles (Perrin and Donovan, 1984). Data were incomplete for several females; therefore they were classified as "unknown females." No information on gender was available for several additional samples; their sex and reproductive status were classified as "unknown."

Identification of prey and calculation of measures of relative importance

A reference collection of otoliths from common Peruvian marine fishes was made from specimens purchased at local markets and identified with Chirichigno's (1978) key. Otoliths from stomach contents were identified by comparison with this collection and collections belonging to the Instituto del Mar del Peru (IMARPE) and to P. Majluf (University of Cambridge). Squid species were identified from their beaks by using published keys (Wolff, 1984; Clarke, 1986), through reference to beaks from local squids identified and supplied by F. Cardoso (Museo de

Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima), and with the assistance of S. Candela (University of Miami, Florida).

Counts and measurements of undigested hard parts of prey allowed calculation of several measures of the relative importance of each prey species. The simplest measure, "percent frequency of occurrence", was defined as 100 multiplied by the number of stomachs in which a prey species was present/the total number of stomachs in the sample, excluding empty stomachs. "Percent total numbers," was defined as 100 multiplied by the number of individuals of a species of prey/the sum of individuals for all prey species (Frost and Lowry, 1980). The number of individuals of each prey species in a sample was estimated by dividing the count of its otoliths (for fish) or squid beaks (for squid) by two (Frost and Lowry, 1980).

Lengths and weights of consumed fish were estimated by using regressions involving fish length and otolith length, or fish weight and either fish length or otolith length. Calculations for anchoveta, *Engraulis ringens*, Pacific Sardine, *Sardinops sagax*, hake, *Merluccius gayi*, and horse mackerel, *Trachurus symmetricus*, followed Chirinos and Chuman (1968), Samame (1977), McKinnon (1988), and Hawes (1983), respectively, except that length was estimated for *T. symmetricus* by using $L=4.37\times W^{1/3}$, and weights of *E. ringens* and *S. sagax* were estimated by using $W=0.007\times L^3$ and $W=0.015\times L^3$, where W=weight (g) and L=total length (cm).[1]

For each fish species, ten randomly selected otoliths from each stomach were measured (Murie, 1984). If fewer than ten suitable otoliths were present, all those available were utilized. Only otoliths with minimal degradation were measured. Degradation was apparent from a loss of detail, particularly the loss or reduction of spines and lobulations along the edges of the otoliths (Frost and Lowry, 1986).

Squid mantle lengths were estimated for each squid species by using linear regressions of mantle length on rostrum length and squid weights from regressions of $\log_e$ weight on $\log_e$ rostrum length (Wolff, 1984). Regressions were not available for patagonian squid, *Loligo gahi*, so regression equations for *Loligo opalescens*, a closely related species, were used (Wolff, 1984). For each squid species, ten randomly selected beaks were measured from each stomach, unless fewer than ten were present, in which case all were utilized.

A mean individual weight (MIW) was calculated for each prey species in each stomach and then used in estimating the percent weight contribution of each prey species to the dusky dolphin's diet. The MIW was usually the mean of the regression-estimated weights of individuals of a given prey species in a particular stomach, unless all hard parts were too degraded to permit reliable measurement, in which case an overall MIW, the mean of all regression-estimated lengths of that species in all stomachs with measurable hard parts, was employed. For anchoveta, however, enough measurable otoliths were available from stomach samples to permit statistical analyses by year and season of capture. Overall MIW's for anchoveta were therefore calculated for each group of stomachs within which analyses revealed no significant differences (for example, the summer of 1985; see Results).

The total weight of each species of squid or fish present in each dolphin stomach was estimated by multiplying the number of individuals present by the appropriate MIW value. The percent weight of each prey species in the dusky dolphin's diet was calculated by using weights summed over all stomachs, as 100 multiplied by the total weight of each prey species/the total weight of all prey present. Species for which regression-estimates of length and weight were not available were excluded from these calculations.

The percent gross energy contribution of each species was defined as 100 multiplied by gross energy of the prey species/summed gross energy of all prey consumed, for all stomach content samples. The gross energy available from a prey species is the caloric density ($kcal\cdot g^{-1}$)×weight (g) consumed. Caloric density (CD) values were obtained from the literature for each prey species, either directly from bomb-calorimetric analyses or indirectly from data on proximate composition, by using CD's for fat, carbohydrate, and protein of 9.4, 4.15, and 5.65 $kcal\cdot g^{-1}$, respectively (Pike and Brown, 1984).

By using published data from non-El Niño years only, CD values for anchoveta were calculated as 1.589 $kcal\cdot g^{-1}$ for the summer and 1.548 $kcal\cdot g^{-1}$ for the winter (Lam, 1968). Data were unavailable for *S. sagax*, but like *E. ringens* it is a clupeoid, and the reproductive seasons of the two species are similar (Muck et al., 1987; Pauly and Soriano, 1987), therefore *S. sagax* was assigned the same seasonal values as *E. ringens*. A value of 1.244 $kcal\cdot g^{-1}$ was calculated for *T. symmetricus* by using proximate composition values from the related *T. trachurus* (Sidwell, 1981). Similarly, a value of 1.158 $kcal\cdot g^{-1}$ for *M. gayi* was based on equivalent data from *M. productus* (Sidwell, 1981). For *Loligo gahi*, 0.968 $kcal\cdot g^{-1}$ was obtained from proximate composition data in Croxall and Prince (1982). No published values were available for *Dosidicas gigas*, so a mean ommastrephid

[1] Pauly, D. International Center for Living Aquatic Resources Management, Manila. Personal commun., 1985.

estimate of 0.922 kcal·g^{-1} was calculated from bomb calorimetric and proximate composition data in Croxall and Prince (1982), Vlieg (1984), and Clarke et al. (1985).

Statistical analyses

Seasonal and annual variation in the size of consumed anchoveta were analyzed with a two-way ANOVA of the mean estimated lengths of the anchoveta in each dolphin stomach, weighted by the number of otoliths measured (SAS, 1985 and 1987). Because of the unbalanced design, sums of squares and *F*-values were calculated by using the "Type III sum of squares" (SAS, 1985). Sidak adjusted *t*-tests were used for comparisons among pairs of means (Sokal and Rohlf, 1981; SAS, 1987). Log-linear analyses were conducted on frequency of occurrence data, also by using SAS (1987), and the resulting *G*-statistics were tested for significance following Sokal and Rohlf (1981).

Data from different locations were pooled for analyses of the effects of year and season on dusky dolphin feeding habits. This was appropriate because the two most distant of the three ports are separated by only about 160 km (Fig. 1), and all three ports are found along the central portion of the Peruvian coast. This region is relatively homogeneous and often treated as a single unit in analyses of oceanographic processes and fish populations (e.g. Brainard and McLain, 1987; Pena et al., 1989). It was necessary to pool data from all locations and collection periods to obtain sample sizes sufficient for analyses of prey occurrence with respect to dolphin reproductive status.

Results

One hundred and thirty-six stomach samples contained recognizable hard parts and were used in subsequent analyses (Table 1). Six additional stomachs were empty, containing no recognizable hard parts at the time of their collection. There were no obvious patterns in the years, seasons, or locations in which the empty stomachs occurred, or the reproductive status of the individuals from which they were obtained (Table 1). Eight additional samples contained otoliths at the time of their collection, according to field notes, but lacked otoliths when examined in the laboratory several months later. These otoliths may have dissolved during storage; therefore these samples were not included in analyses.

Species included in percent weight and percent gross energy calculations—*E. ringens, T. symmetricus, M. gayi, S. sagax, L. gahi* and *D. gigas*—represented the vast majority of prey, over 98% of the total number consumed. Other species, anchoa, *Anchoa* sp., blackruff, *Seriolella violacea*, a flyingfish, *Hirundichthys* sp., and deepsea smelt, *Leuroglossus urotramus*, were found in only trace amounts in stomach contents (Table 2).

Anchoveta was the most important prey species by all measures of relative importance. It accounted for 92.5% of all dusky dolphin prey items by total numbers and was present in 97.8% of stomachs. By weight, anchoveta accounted for 83.8% of prey, and by gross energy, 87.3% (Table 2). No other prey species accounted for more than 5.1% of prey by weight, 2.5% by total numbers, or 4.0% by gross energy, or was found in more than 26.5% of the stomachs examined (Table 2).

Table 1

Distribution of stomach content samples containing otoliths or squid beaks, or both, collected from dusky dolphins, *Lagenorhynchus obscurus*, by year, season, and dolphin reproductive status. Numbers in parentheses represent number of empty stomachs containing neither otoliths nor squid beaks.

			Reproductive status[1]							
Year	Season	Location	ImmF's	RestF's	PregF's	LactF's	UnknF's	Males	Unkn's	Total
1985	Summer	Pucusana	4	0	0	1	0	10	0	15
1985	Winter	Pucusana	0	0	0	1	0	0	0	1
1985	Winter	Ancon	4	7	0	8(1)	4	19(1)	0	42(2)
1986	Summer	Pucusana	1	1	3	5	0	10	0	20
1986	Summer	Cerro Azul	0	0	5	1	0	4(1)	0	10(1)
1986	Winter	Pucusana	4	5	4(1)	5	0	12(1)	4	34(2)
1986	Winter	Cerro Azul	1	2	6	1	0	4(1)	0	14(1)

ImmF's=immature females; RestF's=resting females; PregF's=pregnant females; LactF's=lactating females (including simultaneously pregnant and lactating females; two were collected, one at Ancon in the winter of 1985, one at Pucusana in the summer of 1986); UnknF's=females of unknown reproductive status; Males=all males; Unkn's=individuals of unknown sex

By weight, anchoveta accounted for more than half of all prey consumed in every collection period and its lowest frequency of occurrence was 93.3% (Table 3). The percent weight of *T. symmetricus* in dusky dolphin diets was always low, ranging from 0% in the winter of 1985 to a maximum of 14.5% in the summer of 1986, but frequency of occurrence was more variable, ranging from 0% to 53.3% (Table 3). In a log-linear analysis, the three-way interaction between year, season, and frequency of occurrence of *T. symmetricus* in stomachs was not statistically significant (G=1.91, df=1, P>0.10), nor was the interaction between season and frequency of occurrence significant (G=2.26, df=1, P>0.10). The large increase in frequency of occurrence of this prey from 1985 to 1986, however, resulted in a highly significant interaction between frequency of occurrence and year (G=37.76, df=1, P<0.001). The only other prey found sufficiently often in stomachs for statistical testing of frequency, but not so often that insufficient variation was present (as for anchoveta), was *L. gahi*, for which log-linear analysis yielded a significant three-way interaction between frequency of occurrence, year, and season of collection (G=13.44, df=1, P<0.001). Thus neither season nor year exerted a clear, independent effect on consumption of *L. gahi*, although there was considerable variation among collecting periods (Table 3).

Reproductive status did not have any obvious effect on dusky dolphin feeding habits (Table 4). The frequencies of occurrence of *T. symmetricus* and *L. gahi* did not differ significantly between either lactating females and pooled nonlactating mature females (G=0.39, df=1, P>0.5; G=1.06, df=1, P>0.3, respectively for each prey species) or between lactating females and all other individuals pooled (G=0.29, df=1, P>0.5; G=0.17, df=1, P>0.5, respectively). Anchoveta were consumed by both sexes almost without exception (Table 4).

Table 2

Relative importance of prey species of the dusky dolphin, *Lagenorhynchus obscurus*, from the coastal waters of central Peru in the summers and winters of 1985 and 1986 (n=136 stomachs, 9,137 individual fish and squid). Percent weight and percent gross energy were calculated by using only the six most important prey species.

Prey species	% Frequency of occurrence	% Total numbers[1]	% Weight	% Gross energy
Engraulis ringens	97.8	92.5	83.8	87.3
Trachurus symmetricus	26.5	2.5	3.5	2.9
Merluccius gayi	8.1	0.6	5.1	4.0
Sardinops sagax	4.4	0.2	2.2	2.3
Loligo gahi	19.1	2.2	3.7	2.4
Dosidicas gigas	11.0	0.4	1.6	1.0
Anchoa sp.	1.5	0.1	-	—
Seriolella violacea	1.5	0.0	—	
Hirundichthys sp.	0.7	0.0	—	—
Leuroglossus urotramus	0.7	0.5	—	—
Unknowns[2]	9.6	1.1		—

[1] Percent total numbers values were sometimes very low, e.g. 0.01% or only 0.0% to an accuracy of one decimal place, even when a prey species was present in more than one stomach and its percent frequency of occurrence was greater than 1%.
[2] There appeared to be at least eight species of fish represented among the otoliths which could not be identified

Table 3

Relative dietary contribution of prey species commonly eaten by the dusky dolphin, *Lagenorhynchus obscurus*, for each combination of year and season.

	% Total weight (% Frequency of occurence)			
Prey species	Summer 1985 (n=15)[1]	Winter 1985 (n=43)	Summer 1986 (n=30)	Winter 1986 (n=48)
E. ringens	76.6 (100.0)	86.4 (97.7)	66.0 (93.3)	91.4 (100.0)
T. symmetricus	0.2 (6.7**)	0.0 (0.0**)	14.5 (53.3**)	3.4 (39.6**)
M. gayi	22.0 (13.3)	3.1 (9.3)	6.9 (16.7)	0.0 (0.0)
S. sagax	1.0 (6.7)	0.4 (2.3)	0.9 (3.3)	4.9 (6.3)
L. gahi	0.1 (6.7**)	9.6 (34.9**)	2.3 (26.7**)	0.2 (4.2**)
D. gigas	0.0 (0.0)	0.5 (20.9)	9.4 (16.7)	0.1 (2.1)

[1] n=Number of dusky dolphins from which stomach content samples were collected
**=Significant differences present at P<0.001

Prey size

All dusky dolphin prey species for which lengths and weights could be estimated averaged less than 30 cm (mantle length for the squids, fork length for *M. gayi*, and total length for all others) and 300 g. The

Table 4

Percent composition by weight and frequency of occurrence of prey found in stomach contents of dusky dolphins, *Lagenorhynchus obscurus*, classified by reproductive status. All collection periods are pooled (summers and winters of 1985 and 1986).

		% Weight[2] (% Frequency of occurrence)					
Reproductive status[1]	*n*	*E. ringens*	*T. symmetricus*	*M. gayi*	*S. sagax*	*L. gahi*	*D. gigas*
Imm. Fem.'s	14	74.3	4.6	7.3	0.0	12.9	0.8
		(92.9)	(14.3)	(14.3)	(0.0)	(21.4)	(28.6)
Rest. Fem.'s	15	82.6	0.9	0.0	15.9	0.6	0.0
		(100.0)	(26.7)	(0.0)	(6.7)	(6.7)	(0.0)
Preg. Fem.'s	18	85.7	0.7	0.9	3.0	0.8	8.9
		(100.0)	(33.3)	(5.6)	(11.1)	(16.7)	(16.7)
Lact. Fem.'s	22	87.1	0.7	8.3	0.6	3.0	0.4
		(100.0)	(22.7)	(13.6)	(4.5)	(22.7)	(13.6)
Males	59	81.8	7.5	5.9	0.4	4.0	0.4
		(96.6)	(30.5)	(8.5)	(1.7)	(22.0)	(6.8)

[1] Imm. Fem.'s=immature females; Rest. Fem.'s=resting females; Preg. Fem.'s=pregnant females; Lact. Fem.'s=lactating females, including those simultaneously pregnant and lactating; Males=all males; individuals of unknown reproductive status omitted.
[2] May not total 100 in each row due to rounding.

most common prey species, *E. ringens*, *T. symmetricus*, and *L. gahi*, averaged less than 20 cm and 100 g (Table 5).

The regression-estimated lengths of consumed anchoveta varied significantly with year, season, and the interaction between year and season (F=416.06, 62.56, and 35.42, respectively; df=1, 67, $P \leq 0.0001$; Table 6). In comparisons between pairs of means, anchoveta were found to be significantly larger in the summer and the winter of 1986 than in either the summer or the winter of 1985 (Table 6). In 1985, otolith lengths were significantly different between summer and winter, but not in 1986 (Table 6).

Mean total lengths of anchoveta from fishery samples (for each combination of year and season) were positively correlated with mean regression-estimated lengths of anchoveta consumed by dusky dolphins (r=0.98, df=2, P<0.05; Table 6). Mean estimates of total length for anchoveta consumed by dusky dolphins were consistently 1.4–2.0 cm smaller than mean total lengths of anchoveta taken by the fishery, however (paired t-test, t=12.4, df=3, P<0.01).

Table 5

Mean lengths (cm) and weights (g), as estimated from regressions on otolith length/radius and squid beak rostrum length, of fish and squid species commonly found in the stomachs of the dusky dolphin, *Lagenorhynchus obscurus*, landed along the central Peruvian coast in 1985 and 1986.

	Estimated mean length (SE)		Estimated mean weight (SE)	
Prey species	No. of hard parts[4]	(No. of stomachs)[5]	No. of hard parts[4]	(No. of stomachs)[5]
E. ringens[1]	13.4	(0.14)	17.3	(0.49)
	593	(71)	593	(71)
S. sagax[1]	25.1	(0.32)	237.0	(8.67)
	4	(2)	4	(2)
M. gayi[2]	25.2	(4.62)	198.0	(104.0)
	18	(5)	18	(5)
T. symmetricus[1]	11.5	(1.16)	25.6	(8.67)
	34	(13)	34	(13)
L. gahi[3]	13.0	(0.27)	33.3	(1.23)
	97	(26)	97	(26)
D. gigas[3]	13.4	(1.00)	72.7	(16.4)
	34	(15)	34	(15)

[1] Total length.
[2] Fork length.
[3] Mantle length.
[4] Number of hard parts measured.
[5] Number of stomachs from which samples were taken.

Discussion

The prey of the dusky dolphin in Peruvian coastal waters can be characterized as schooling, small to medium size, pelagic or semi-pelagic species (*M. gayi* is usually demersal but sometimes forms large pelagic schools [Mejía and Jordán, 1979]). Anchoveta was typical and was unequivocally the most important prey species in 1985–86. It was most important by all measures of consumption and constituted almost 90% of the dusky dolphin's diet by percent gross

Table 6

Mean estimated total lengths of anchoveta, *Engraulis ringens*, consumed by dusky dolphins, *Lagenorhynchus obscurus*, in central Peruvian coastal waters in 1985 and 1986, compared to mean lengths of anchoveta taken in the purse-seine fishery.

Collection source	Summer 1985	Winter 1985	Summer 1986	Winter 1986
Stomachs of dusky dolphins				
Mean estimated total length of anchoveta[1] (SE)	11.5[a] (0.14)	12.9[b] (0.09)	14.1[c] (0.10)	14.3[c] (0.07)
Number of otoliths measured	112	150	103	228
Number of stomachs from which otoliths were collected	12	18	14	27
Purse-seine fishery				
Mean total length of anchoveta[2]	13.5	14.6	15.5	16.3

[1] Based upon measurements of otoliths in dusky dolphin stomachs.
[2] Mean total length of anchoveta taken in the fishery, calculated from data in Pauly and Palomares (1989); SE's and *N*'s unavailable.
[a,b,c] Means with different letters in the superscript differed significantly (Sidak adjusted *t*-tests; $t \geq 8.41$, $P < 0.001$ in all cases) while those with the same letter did not ($t = 1.42$, $P > 0.5$).

energy, usually considered the best measure of relative prey importance (Lavigne et al., 1982). Few data are available on feeding habits for other regions, but in Argentina dusky dolphins also fed on a species of anchovy (Würsig and Würsig, 1980).

There were no consistent seasonal patterns in prey consumption in the present study. Rather, anchoveta was the most important prey species in both seasons of both years, probably owing, in part, to its relatively high abundance throughout the study period (Pauly and Palomares, 1989). Consumption of *T. symmetricus* was more variable and opportunistic. In 1985 *T. symmetricus* was almost absent from stomach samples, but it was a major prey item in 1986 when unusually large numbers of juveniles, similar in size to other important dusky dolphin prey, were observed in the coastal waters of central and northern Peru (IMARPE et al., 1986). Other species, particularly *L. gahi*, varied greatly among collection periods in their importance as prey, but did not exhibit consistent seasonal or annual patterns.

In examining the effects of season, year, and other variables on diet, only frequency of occurrence was analyzed statistically because analyses of other measures of prey importance involve excessive violations of the assumptions underlying most statistical tests (Recchia and Read, 1989). Percent-weight estimates were used for qualitative comparisons among collection periods and reproductive classes, rather than percent gross energy values, because the latter were very gross approximations.

Anchoveta was the main prey of all reproductive classes of dusky dolphins. In contrast, in the eastern tropical Pacific most spotted dolphins, *Stenella attenuata*, eat mainly ommastrephid squids whereas lactating females eat principally fish (Bernard and Hohn, 1989). The greater energy and water requirements of lactating females may force them to feed on fish, which contain more energy and water per unit weight than squid or, alternatively, the presence of a calf may prevent females from feeding at the depths at which squid occur (Bernard and Hohn, 1989). In Peru, lactating dusky dolphins were apparently able to satisfy their energy and water requirements, as did other females, males and juveniles, by feeding on the abundant, high energy anchoveta (Lam, 1968).

Like the fishermen, fur seals, and seabirds of the Peruvian coast, dusky dolphins were somewhat opportunistic in their feeding in respect to the sizes of the anchoveta they preyed upon, taking more of the more abundant size classes (Muck and Pauly, 1987; Majluf, 1989). Anchoveta consumed by dusky dolphins were consistently 1.4–2.0 cm smaller, however, than those taken in the fishery, perhaps because of the fishery's bias towards larger anchoveta (Palomares et al., 1987). Alternatively, the slight degradation present in some of the otoliths from which anchoveta sizes were estimated may have resulted in underestimation of total lengths (Recchia and Read, 1989). The observed discrepancy may also be due to variation in the relationship between otolith size and body size, which can differ among years because of variation in growth rates of fish (McKinnon, 1988; Reznick et al., 1989; Secor and Dean, 1989; Campana, 1990).

Relative consumption of fishes with small otoliths, such as anchoveta, may have been underestimated. Large otoliths and squid beaks are less easily dissolved by stomach acids than are smaller otoliths (Hawes, 1983; Bigg and Fawcett, 1985; da Silva and

Neilson, 1985; Recchia and Read, 1989) and squid beaks are less easily passed through the digestive tract than are otoliths (Hawes, 1983; Bigg and Fawcett, 1985). This potential bias tends to strengthen the principal finding of this study: anchoveta was by far the most important prey species of all reproductive classes of Peruvian dusky dolphins in the summers and winters of 1985–86.

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Literature cited

Bernard, H. J., and A. A. Hohn.
1989. Differences in feeding habits between pregnant and lactating spotted dolphins (*Stenella attenuata*). J. Mamm. 70:211–215.

Bigg, M. A., and I. Fawcett.
1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). *In* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne (eds.), Marine mammals and fisheries, p. 284–291. Allen and Unwin, London, 354 p.

Brainard, R. E., and D. R. McLain.
1987. Seasonal and interannual subsurface temperature variability off Peru, 1952–1984. *In* D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change, p. 14–45. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, Manila, 351 p.

Campana, S. E.
1990. How reliable are growth back-calculations based on otoliths. Can. J. Fish. Aquat. Sci. 47:2219–2227.

Chirichigno F., N.
1978. Clave para identificar los peces marinos del Perú. Informe Inst. Mar Perú-Callao 44, Biblioteca, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú, 387 p.

Chirinos de Vildoso, A., and E. Chumán D.
1968. Validez de la lectura de otolitos para determinar la edad de la anchoveta (*Engraulis ringens*). Informe Inst. Mar Perú-Callao 22, Biblioteca, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú, 34 p.

Clarke, A., M. R. Clarke, L. J. Holmes, and T. D. Waters.
1985. Calorific values and elemental analysis of eleven species of oceanic squids (Mollusca: Cephalopoda). J. Mar. Biol. Ass. U.K. 65:983–986.

Clarke, M. R. (ed.)
1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford, 273 p.

Croxall, J. P., and P. A. Prince.
1982. Calorific content of squid (Mollusca: Cephalopoda). Br. Antarct. Surv. Bull. 55:27–31.

da Silva, J., and J. D. Neilson.
1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. Can. J. Fish. Aquat. Sci. 42:1439–1442.

Frost, K. J., and L. F. Lowry.
1980. Feeding of ribbon seals (*Phoca fasciata*) in the Bering Sea in spring. Can. J. Zool. 58:1601–1607.
1986. Sizes of walleye pollock, *Theragra chalcogramma*, consumed by marine mammals in the Bering Sea. Fish. Bull. 84:192–197.

Gaskin, D. E.
1972. Whales, dolphins and seals—with special reference to the New Zealand region. St. Martin's Press, New York, 200 p.
1982. The ecology of whales and dolphins. Heinemann, London, 459 p.

Goodall, R. N. P., and A. R. Galeazzi.
1985. A review of the food habits of the small cetaceans of the Antarctic and the sub-Antarctic. *In* W. R. Siegfried, P. R. Condy, and R. M. Laws (eds.), Antarctic nutrient cycles and food webs, p. 566–572. Springer-Verlag, Berlin, 700 p.

Hawes, S. D.
1983. An evaluation of California sea lion scat samples as indicators of prey importance. Unpubl. M.A. thesis, San Francisco State Univ., 50 p.

IMARPE, SENAMHI, DHNM, and IGP.
1986. Condiciones bio-oceanográficas y meteorológicas frente a la costa Peruana en Enero-Junio 1986. ERFEN Boletín 19:3–11, Comisión Permanente del Pacífico Sur, Calle 76 No. 9, 88 Apartado Aereo 92292 Bogotá, Colombia.

Lam, R.
1968. Estudio sobre la variación del contenido de grasa en la anchoveta Peruana (*Engraulis ringens* J.). Informe Inst. Mar Perú-Callao 24, Biblioteca, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú, 29 p.

Lavigne, D. M., W. Barchard, S. Innes, and N. A. Oritsland.
1982. Pinniped bioenergetics. *In* J. G. Clarke (ed.), Mammals in the seas, Vol. IV: small cetaceans, seals, sirenians and otters, p. 191–235. FAO Fisheries Series Number 5, Rome, 531 p.

Majluf, P.
1989. Reproductive ecology of South American fur seals in Peru. *In* D. Pauly, P. Muck, J. Mendo and I. Tsukayama (eds.), The Peruvian upwelling ecosystem: dynamics and interactions, p. 332–343. Conference Proceedings 18. ICLARM, IMARPE, GTZ, 438 p.

McKinnon, J. S.
1988. Feeding habits of three species of small cetaceans from the coastal waters of Perú. Unpubl. M.S. thesis, Univ. Guelph, 94 p.

Mejía G., J., and R. Jordán S.
1979. La situación actual del stock de merluza a setiembre de 1978. Informe Inst. Mar Perú-Callao 57, Biblioteca, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú, 19 p.

Muck, P., and D. Pauly.
1987. Monthly anchoveta consumption of guano birds, 1953 to 1982. *In* D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change, p. 219–233. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, 351 p.

Muck, P., O. Sandoval de Castillo, and S. Carrasco.
1987. Abundance of sardine, mackerel and horse mackerel eggs and larvae and their relationship to temperature, turbulence and anchoveta biomass off Peru. *In* D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change, p. 268–275. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, 351 p.

Murie, D. J.
1984. Estimating food consumption of free-living harp seals, *Phoca groenlandica* (Erxleben 1777). Unpubl. M.S. thesis, Univ. Guelph, 97 p.

Murie, D. J., and D. M. Lavigne.
1985. A technique for the recovery of otoliths from stomach contents of piscivorous pinnipeds. J. Wildl. Manage. 49:910–912.

Palomares, M. L., P. Muck, J. Mendo, E. Chumán, O. Gómez, and D. Pauly.
1987. Growth of the Peruvian anchoveta (*Engraulis ringens*), 1953 to 1982. *In* D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change, p. 117–141. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, 351 p.

Pauly, D., and M. L. Palomares.
1989. New estimates of monthly biomass, recruitment and related statistics of anchoveta (*Engraulis ringens*) off Peru (4–14°S), 1953–1985. *In* D. Pauly, P. Muck, J. Mendo, and I. Tsukayama (eds.), The Peruvian upwelling ecosystem: dynamics and interactions, p. 189–206. Conference Proceedings 18. ICLARM, IMARPE, GTZ, 438 p.

Pauly, D., and M. Soriano.
1987. Monthly spawning stock and egg production of Peruvian anchoveta (*Engraulis ringens*), 1953 to 1982. *In* D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change, p. 167–178. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, 351 p.

Pauly, D., and I. Tsukayama (eds.).
1987. The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. ICLARM, IMARPE, GTZ, 351 p.

Pauly, D., P. Muck, J. Mendo, and I. Tsukayama (eds.).
1989. The Peruvian upwelling ecosystem: dynamics and interactions. Conference Proceedings 18. ICLARM, IMARPE, GTZ, 438 p.

Peña, N., J. Mendo, and J. Pellón.
1989. Sexual maturity of Peruvian anchoveta (*Engraulis ringens*), 1961–1987. *In* D. Pauly, P. Muck, J. Mendo, and I. Tsukayama (eds.), The Peruvian upwelling ecosystem: dynamics and interactions, p. 132–142. Conference Proceedings 18. ICLARM, IMARPE, GTZ, 438 p.

Perrin, W. F., and G. P. Donovan.
1984. Report of the workshop. Rep. Int. Whaling Comm. Spec. Issue 6:1–24.

Perrin, W. F., R. R. Warner, C. H. Fiscus, and D. B. Holts.
1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed species aggregations. Fish. Bull. 71:1077–1092.

Pike, R. L., and M. L. Brown.
1984. Nutrition, an integrated approach, 3rd ed. John Wiley & Sons, New York, 1068 p.

Read, A. J., K. Van Waerebeek, J. C. Reyes, J. S. McKinnon, and L. C. Lehman.
1988. The exploitation of small cetaceans in coastal Peru. Biol. Cons. 46:53–70.

Recchia, C. A., and A. J. Read.
1989. Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. Can. J. Zool. 67:2140–2146.

Reznick, D., E. Lindbeck, and H. Bryga.
1989. Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). Can. J. Fish. Aquat. Sci. 46:108–112.

Ryther, J. H.
1969. Photosynthesis and fish production in the sea. Science 166:72–76.

Samamé L., M.
1977. Determinación de la edad y crecimiento de la sardina *Sardinops sagax sagax* (J). Boletín Inst. Mar Perú-Callao 3:95–112. Biblioteca, Instituto del Mar del Perú, P.O. Box 22, Callao, Perú.

SAS.
1985. SAS user's guide: statistics, version 5. SAS Institute, Cary, NC, 956 p.
1987. SAS/STAT guide for personal computers, version 6. SAS Institute, Cary, NC, 378 p.

Secor, D. H., and J. M. Dean.
1989. Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. Can. J. Fish. Aquat. Sci. 46:113–121.

Sidwell, V. D.
1981. Chemical and nutritional composition of finfishes, whales, crustaceans, mollusks and their products. Dep. Commer., NOAA Tech. Memo. NMFS F/SEC-11. Available from National Technical and Information Service, 5285 Port Royal Rd., Springfield, VA 22161, 440 p.

Sokal, R. R. and F. J. Rohlf.
1981. Biometry. W. H. Freeman and Company, New York, 859 p.

Treacy, S. D., and T. W. Crawford.
1981. Retrieval of otoliths and statoliths from gastrointestinal contents and scats of marine mammals. J. Wildl. Man. 45:990–993.

Van Waerebeek, K., and J. C. Reyes.
1990. Catch of small cetaceans at Pucusana port, central Peru, during 1987. Biol. Cons. 51:15–22.

Vlieg, P.
1984. Proximate composition of New Zealand squid species. N. Z. J. Sci. 27:145–150.

Wolff, G. A.
1984. Identification and estimation of size from the beaks of 18 species of cephalopods from the Pacific Ocean. Dep. Commer., NOAA Tech. Rep. NMFS 17. Available from National Technical and Information Service, 5285 Port Royal Rd., Springfield, VA 22161, 50 p.

Würsig, B., and M. Würsig.
1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. Fish. Bull. 77:871–890.

Abstract.—This study examines the early life history of a population of walleye pollock, *Theragra chalcogramma* (Pallas), that is found in Resurrection Bay, Alaska. Ichthyoplankton samples were taken at six stations in Resurrection Bay during early May and early June 1989 along with hydrographic data. Standard lengths of all walleye pollock were measured, and subsamples from two stations were aged by using otolith increments for growth rate and hatch date analysis. Abundances ranged from 60 to 575 larvae m^{-2} in May and from 0 to 10 larvae m^{-2} in June with densities of up to 12 larvae m^{-3} in May. The estimated growth rate was 0.18 mm/day. Back-calculated hatch dates ranged from late March until early May; the median hatch date was 22 April. Comparisons of abundance and growth rate to values from other habitats indicate that this deep fjord provides a suitable habitat for larval walleye pollock. Hydrographic data and larval size distribution suggest that advection plays a major role in determining the distribution of larvae in the fjord.

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Distribution, abundance, and growth of larval walleye pollock, *Theragra chalcogramma*, in an Alaskan fjord

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Fjords have long been recognized as nursery grounds for many commercially important fish species (De Silva, 1973; Lie, 1978; Carmo Lopes, 1979). Matthews and Heimdal (1980) in their review of food chains in fjords pointed out that many fjords along Scandinavian, Scottish, and North American coasts are highly productive areas. The productivity of fjords is often enhanced by hydrographic boundary conditions or land runoff that can increase nutrient levels (Matthews and Heimdal, 1980). Production in fjords may be further enhanced by upwelling conditions at their mouths. This is especially true for the southern coast of Alaska, where the relaxation of easterly winds in summer promotes coastal divergence and upwelling (Royer, 1982).

Rogers et al. (1987) described the nearshore zone of the Gulf of Alaska as an important spawning or rearing area, or both, for several commercially important fish species, including walleye pollock, *Theragra chalcogramma*. However, no work has been done to examine the dynamics of early life history stages of walleye pollock or other fishes in Alaskan fjords.

We chose walleye pollock for this study because it was more abundant than any other species in Resurrection Bay (Smith et al., 1991) and its development and early life history in other areas of the Gulf of Alaska are well known (Dunn and Matarese, 1987; Kendall et al., 1987; Kim, 1989). Furthermore, it is very important commercially, with annual landings off Alaska exceeding one million metric tons (Lloyd and Davis, 1989), and the walleye pollock resource shows high fluctuations in year-class strength (Megrey, 1991), which creates a strong incentive to determine possible causes.

Most of the research on pollock in the Gulf of Alaska has been focused on the Shelikof Strait region (Schumacher and Kendall, 1991), while other areas along the Gulf, except for Auke Bay in Southeast Alaska (Haldorson et al. 1989, a and b), have received little attention. Although the Shelikof Strait spawning area is believed to be the most important in the Gulf of Alaska (Hinckley et al., 1991), substantial pollock spawning occurs in other areas of the Gulf (Müter, 1992; Norcross and Frandsen[1]).

Resurrection Bay shares many features with other embayments along the southcentral coast of Alaska and can be considered representative of the area. This study used growth analysis together with

[1] Norcross, B. L., and M. Frandsen. Distribution and abundance of larval fishes in Prince William Sound, Alaska, during 1989 after the *Exxon Valdez* oil spill. EVOS Symposium Proceedings. Am. Fish Soc. Symposium. In review.

distribution and abundance data to evaluate the role of this northern Gulf of Alaska fjord in the early life history of walleye pollock. Specifically, the objectives of this study were 1) to determine the distribution and abundance of walleye pollock larvae in a glaciated fjord, 2) to quantify growth rates of larvae within this fjord and compare growth rates to literature values from other areas, and 3) to estimate hatch dates of the observed population.

Materials and methods

Resurrection Bay is a fjord approximately 32 km long and 4–8 km wide, located within the coastal mountain range on the Kenai Peninsula on the south-central coast of Alaska (Fig. 1). The fjord's bathymetry shows an inner basin with a maximum depth of 300 m, separated by a sill from the outer basin. The sill is located about 15 km from the fjord's mouth at the narrowest point, between our sampling stations RES 2.5 and RES 3 (Fig. 1), and rises to a depth of approximately 185 m. The outer basin is slightly shallower (265 m) than the inner basin and has an open connection with the shelf.

Six stations were sampled along the fjord axis (Fig. 1) during two cruises, 1–4 May 1989 and 7–9 June 1989. Ichthyoplankton samples for this study were collected from the RV *Little Dipper*, a 9-m aluminum boat. Horizontal plankton tows were taken at discrete depths by using a 1-m^2 Tucker trawl, rigged with two 505-μ mesh nets. Because no previous data were available we took samples throughout the water column. We tried to obtain at least one sample from each of the following depth strata per station: 0–15 m, 15–30 m, 30–50 m, 50–80 m, 80–150 m, and 150-m to the bottom. Because of weather and time constraints, fewer samples were taken at some stations. Sample depths were initially estimated from wire angle and length of extended wire. Actual depths were recorded with an attached Seabird Seacat conducting-temperature-depth (CTD) (SBE 19) profiler and retrieved after completion of the cruise. The nets were rigged to a double tripper which allowed the second net to be opened and closed via a messenger from the surface. The net was towed for five minutes in the direction of tidal flow at a towing speed of 1.5 to 2.5 knots. Only daytime tows were made. Volume filtered during each tow was calculated from a TSK or General Oceanics flowmeter that was attached in a central position to the mouth of the net. Samples used for this analysis were immediately preserved in 50% isopropyl alcohol or 95% ethyl alcohol. The alcohol was renewed for each sample after 24 hours and after 2–3 days. Because differential shrinkage was observed between preservatives, only larvae preserved in isopropyl alcohol were used in size comparisons.

A Seabird CTD Profiler was attached to the net during most tows to record conductivity, temperature, and pressure throughout the tow. When no CTD data were recorded, depth was estimated from the wire angle and the length of extended wire. In addition, CTD data were taken at each station and along cross-fjord transects through each station. Because of equipment failure, no temperature and salinity data were obtained during the June cruise. Additional CTD-profiles for RES 2.5 and GAK 1 were obtained from a cruise on 6 April of the same year.

Samples were sorted in the laboratory to isolate finfish larvae. Walleye pollock larvae were identified and measured to standard length (SL). Densities in larvae·m^{-3} were calculated and abundance in larvae·m^{-2} at each station was estimated by integrating larval densities over the water column by using vertical distribution profiles. Density was set to zero at the surface and was assumed to change in a linear fashion between successive sampling depths. Be-

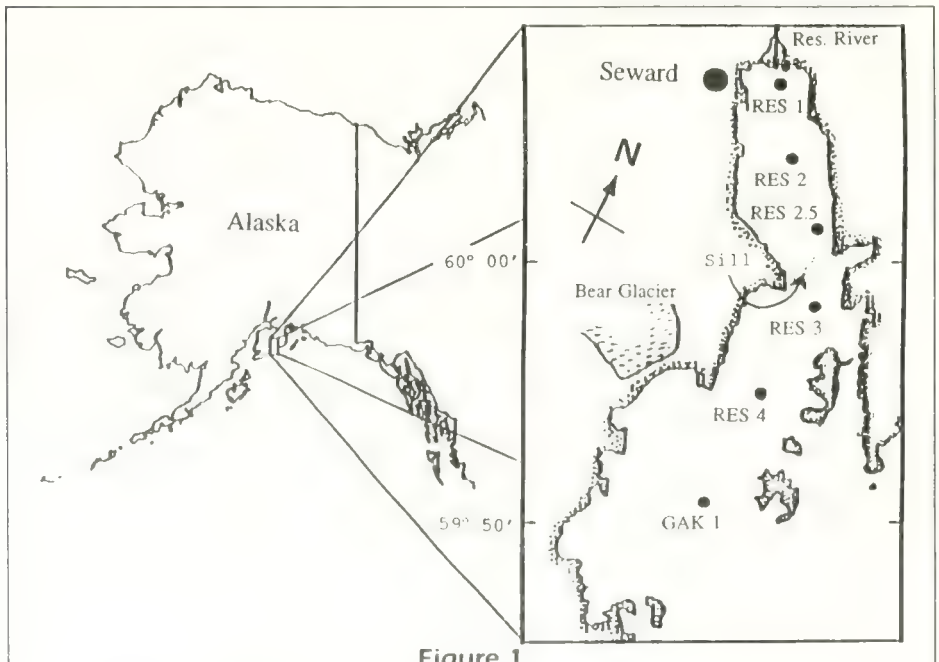

Figure 1
Map of Alaska and Resurrection Bay including stations sampled.

cause no replicate samples were taken, confidence limits could not be calculated.

A Student *t*-test (two-sample comparison) or a one-way ANOVA followed by a Tukey multiple comparison test (multiple samples) was employed to detect differences in mean standard length of larvae among different depths at the same station and among different stations. Nonparametric tests were employed in addition to parametric test procedures when the assumptions for parametric tests were violated. The nonparametric tests used were a Kruskal-Wallis test (nonparametric analysis of variance), a Mann-Whitney test (two-sample comparison), and a Tukey-type multiple comparison test (Zar, 1984).

Differences in larval length among stations were examined by using the most shallow samples from each station (<22 m), thus minimizing potential errors resulting from differences in size due to vertical distribution. In addition, pollock lengths from all depths were pooled for each station and the mean of the pooled data was compared between stations. For all between-station comparisons, larval mean SL was corrected for the date of sampling by using growth rates obtained during this study.

Ages of larvae were estimated from the number of otolith increments on sagittal otoliths as described in Kendall et al. (1987). Increments were independently counted a second time by the same reader. Readings were confirmed for a subsample of 20 otoliths by the Alaska Fisheries Science Center laboratory in Seattle, Washington. Only those independent readings that did not differ by more than one increment (in which case the higher count was used) were used for growth determination. Random subsamples of larvae from two stations, one in the inner basin (RES 2) and one in the outer basin (RES 4) were aged. Only larvae from these stations could be aged because otoliths from all other samples showed signs of erosion.

Larval growth rates were determined by fitting linear regression lines to length-at-age data. The linear regression equations describing growth were compared between stations to test for differences in regression coefficients. Slopes and elevations were compared by using Student's *t*-statistic (Zar, 1984). Hatch dates were estimated after correcting for mortality, because older fish in the sample experienced a higher cumulative mortality than larvae hatched closer to the date of sampling. Following Yoklavich and Bailey (1990), we created a stepped, size-specific mortality function with rates of 0.1, 0.08, 0.06, 0.03 per day for fish <7, 7.01–10.0, 10.01–15.0 and 15.01–20.0 mm SL, respectively. The range of ages corresponding to each size range was calculated from the growth equation obtained in this study. The hatch date distribution was then estimated by backcalculating numbers of larvae at hatching for each daily cohort with the above mortality rates.

Results

Hydrography of the fjord

On 6 April 1989, temperatures at RES 2.5 (inner basin) and GAK 1 (mouth of fjord) increased with depth from approximately 4°C in the surface layer to almost 6°C below 200 m (Fig. 2). Between April and May 1989 the properties of the water masses inside and outside the fjord changed considerably. In April the upper 100 m were nearly homogenous, but a strong seasonal thermocline had developed between 10 and 20 m in early May. The surface temperature in May varied between 5.8°C at RES 2.5 and 7°C at RES 3 (Fig. 2). Temperature profiles in May showed a pronounced minimum of about 3.5°C to 4.5°C near 80 m. While temperatures in April in

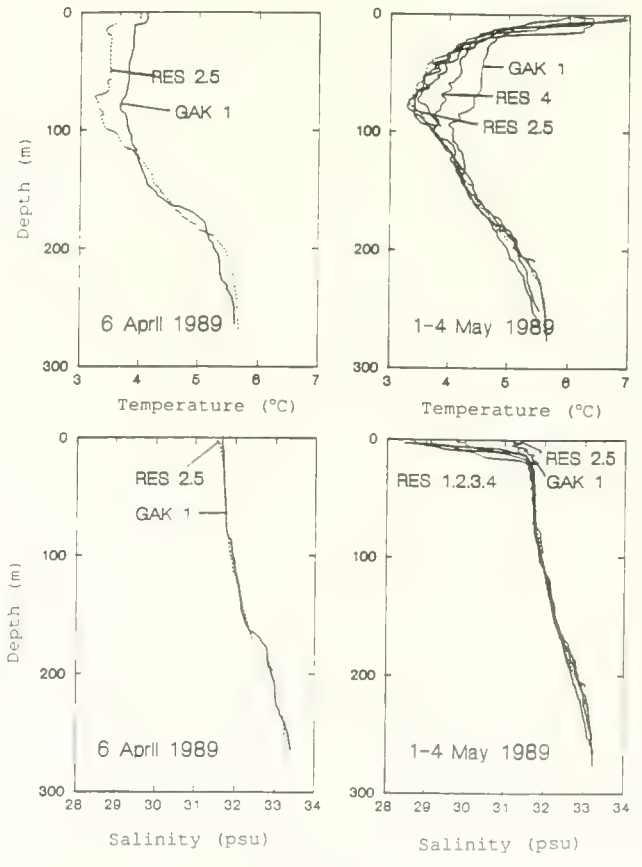

Figure 2

Temperature and salinity profiles at six stations in Resurrection Bay, Alaska, 6 April and 1–4 May 1989.

the upper 100 m did not differ by more than 0.5°C between RES 2.5 and GAK 1, the temperature difference in May was almost 1.5°C.

The water column was nearly isohaline in April: salinity increased approximately 1.5 psu (practical salinity unit) from surface to bottom. Salinity profiles in May show a well-developed low salinity surface layer at four of the stations (Fig. 2), resulting from river runoff and snow melt. The surface salinities were 2 to 4 psu lower than in April. However, at RES 2.5 and GAK 1 the freshwater lens was much less developed than at the other stations. The surface layer salinity was above 31 psu and almost identical at both stations. Below the halocline, salinities were very similar at all stations.

Distribution and abundance

In early May, walleye pollock larvae were caught at all stations and sampled at all depths. A total of 16,950 pollock larvae were collected in 39 tows at depths between 7 and 280 m. Larval densities ranged from 0.03 larvae·m^{-3} (RES 4, 105 m) to a maximum of 11.9 larvae·m^{-3} (RES 4, 26 m). Larvae were generally concentrated in the upper 70 m (Fig. 3). Maximum densities occurred at depths between 18 and 30 m at all stations, except GAK 1, and ranged from 2.2 larvae·m^{-3} to 11.9 larvae·m^{-3}. Pollock larvae were distributed deeper in the water column outside the sill, at stations RES 4 and GAK 1, than at stations inside the sill (Fig. 3).

Between May and June, larval densities decreased by two orders of magnitude and ranged from 0 to 0.4 larvae·m^{-3} in early June (Fig. 4). In June, a total of 420 walleye pollock larvae were collected in 45 tows at depths between 5 and 250 m. Only tows above 75 m caught pollock larvae. Vertically, the maximum in larval density occurred between 10 m (RES 1) and 58 m (RES 3). The vertical distribution in early June showed no apparent pattern in relation to station location (Fig. 4).

Using vertical distribution profiles, we estimated larval abundance at each station. In May, estimated abundances ranged from 60 larvae·m^{-2} at RES 1 to 575 larvae·m^{-2} at GAK 1 (Table 1). Abundances at the outer stations were much higher than in the inner basin owing to high larval densities below 50 m at RES 4 and GAK 1.

In June abundances ranged from 0.5 larvae·m^{-2} at RES 1 to 10.3 larvae·m^{-2} at RES 3. The estimated abundances were again higher at the outer stations. The highest abundance was found above the sill, as

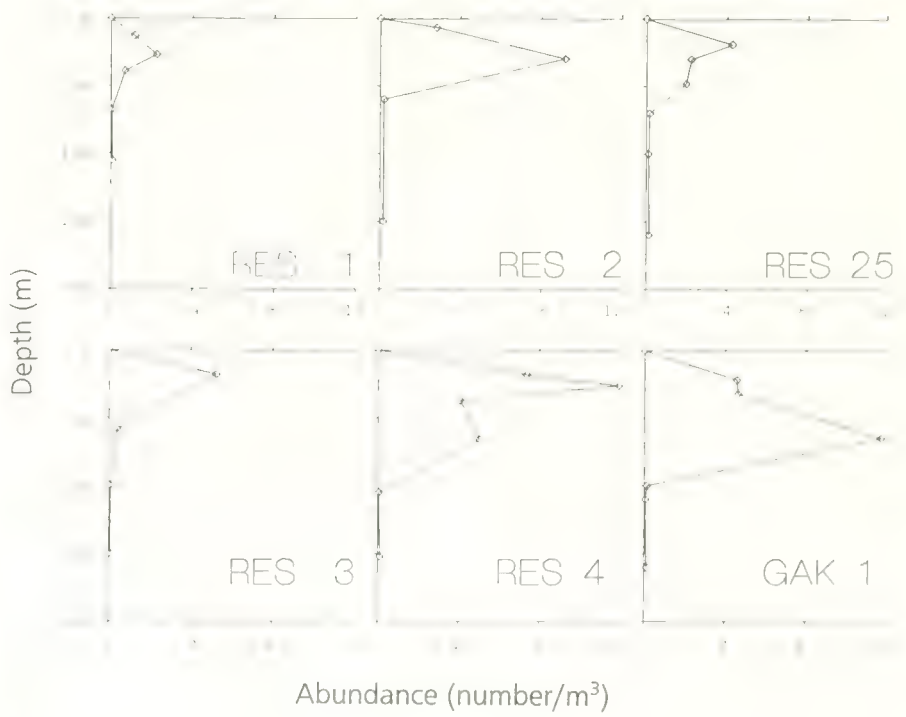

Figure 3

Vertical distribution of walleye pollock larvae, *Theragra chalcogramma*, in Resurrection Bay, Alaska, 1–4 May 1989.

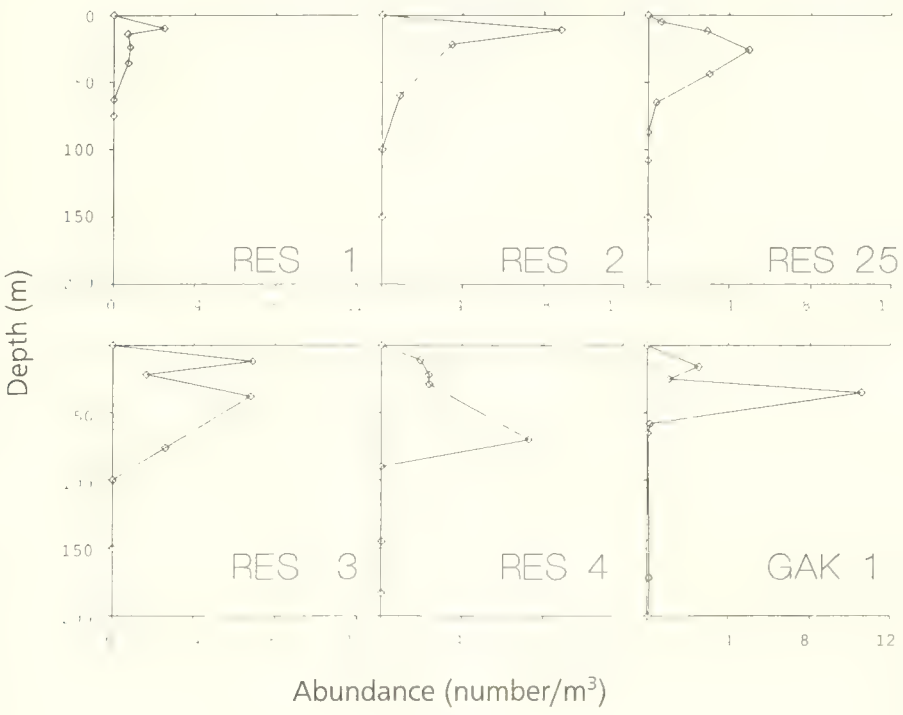

Figure 4

Vertical distribution of walleye pollock larvae, *Theragra chalcogramma,* in Resurrection Bay, Alaska, 7–9 June 1989.

the largest number of larvae was captured at RES 3 at 58 m. Abundance averaged across all stations decreased from 281 larvae·m^{-2} in early May 1989 to 4.6 larvae·m^{-2} five weeks later.

Larval size distribution

Mean SL of larvae differed significantly with depth at all stations in early May (Table 2). Both a *t*-test and a Mann-Whitney test of differences between means showed highly significant differences between the shallow and deep samples at RES 1, 2, 2.5, 3, and RES 4 ($P<0.01$). An ANOVA for station GAK 1 suggested highly significant differences as well ($F=42.33$; $P<0.001$). Results from a Tukey HSD test showed significant differences in mean standard length between the samples from 22 m and 65 m at GAK 1 ($P=0.01$). Differences between any of the remaining pairs at GAK 1 were not significant.

While significant differences in size with depth existed at all stations, the sign of the differences varied between stations. At the two innermost stations (RES 1 and RES 2) larval size decreased with depth, whereas at all other stations the opposite trend was found, i.e. larval size increased with depth, excluding the sample from 100 m at GAK 1. This sample showed a slight decrease in mean SL compared to shallower samples, but the difference was not significant.

To compare larval size between stations, mean SL was corrected for sample date by using observed growth rates. Since we sampled over a four-day period, the measured lengths differed because of growth during this period. Thus, standard length was corrected for date of sampling by using a growth rate of 0.18 mm/day, the overall growth rate of pollock larvae in Resurrection Bay (this study). Table 2 shows

Table 1

Abundance of larval walleye pollock, *Theragra chalcogramma*, in Resurrection Bay in early May and early June 1989.

	Abundance (larvae·m^{-2})	
Station	May	June
RES 1	60	0.5
RES 2	285	4.0
RES 2.5	137	1.8
RES 3	168	10.3
RES 4	461	5.2
GAK 1	575	5.8

mean SL, variance, and corrected mean SL for all samples collected in the upper 100 m. The corrected mean SL will be hereafter referred to as mean SL.

A nonparametric ANOVA by ranks showed that mean SL differed significantly between the shallow samples from each station (Kruskal-Wallis test statistic=746.5, $P<0.001$). A Tukey type nonparametric multiple comparison (Zar, 1984) indicated significant differences ($P<0.05$) between the innermost station pair (RES 1 and RES 2) and each of the stations outside RES 2 (RES 2.5, 3, 4, GAK 1). Among the outside stations, the only significant difference was found between RES 3 and GAK 1 ($P=0.003$).

When samples from all depths were pooled and mean SL compared between stations, results were very similar. An ANOVA showed a highly significant difference in mean SL between the stations ($F=80.00$, $P<0.001$). A Tukey HSD multiple comparison again indicated that significant differences ($P<0.05$) exist between both of the two innermost stations and any one of the stations outside RES 2.

Table 2

Range, mean, standard length (SL), variance, and mean SL corrected for date of sampling for larval walleye pollock, *Theragra chalcogramma*, collected in early May 1989 and preserved in isopropyl alcohol.

Station	Depth (m)	Number of larvae	Range (mm)	Mean SL (mm)	Variance	Corrected mean SL
RES 1	13	188	4.81–10.20	7.75	1.15	7.39
	39	91	4.49–9.31	6.81	0.85	6.45
RES 2	7	481	4.07–15.03	7.61	2.01	7.25
	60	24	4.59–8.40	6.67	1.02	6.31
RES 2.5	19	678	2.65–9.69	5.76	1.17	5.58
	90–110	36	5.22–8.93	6.50	0.62	6.32
RES 3	18	919	3.37–10.68	6.27	1.18	6.09
	58	95	4.15–9.58	6.91	0.88	6.73
RES 4	18	730	3.78–9.15	5.85	0.86	5.85
	66	735	3.58–8.31	6.09	0.50	6.09
GAK 1	22	983	2.87–8.81	5.37	0.78	5.55
	32	299	3.62–7.88	5.45	0.71	5.63
	65	2534	3.80–8.61	5.90	0.40	6.08
	100	29	4.31–6.84	5.65	0.37	5.83

Larvae at stations RES 1 and RES 2 were significantly larger and older than those at stations outside RES 2. The observed size differences translate into an age difference of 8.5 days between the average at the two inner stations (RES 1 and RES 2) and that at the outer stations (RES 2.5, 3, 4, and GAK 1). Age was calculated by using growth equations obtained in this study. The average age of larvae collected at stations RES 1 and RES 2 was estimated at 15.1 days. The average age of larvae at the other four stations was estimated to be 6.6 days, relative to 2 May. Thus, the results of size and age comparisons suggest that the stations can be divided into two distinct groups on the basis of larval size.

Growth rates

Growth rates were determined for larvae collected 1–4 May 1989 at station RES 2 in the inner basin and at station RES 4 in the outer basin. At station RES 2, 62 larvae collected at 7 m on 4 May 1989 were measured and dissected to remove otoliths, of which 54 could be aged. The increment count ranged from 6 to 40 increments for larvae between 5.1 mm and 11.1 mm SL. A linear regression model relating mean SL and increment count yielded a growth rate of 0.18 ± 0.028 mm/day (95% CI)($r^2=0.75$, Fig. 5), assuming each increment represents growth of one day. From a sample collected at RES 4, at 18 m on 2 May 1989, 38 larvae ranging in length from 5.3 mm to 10.1 mm were aged. The growth rate at this station was estimated to be 0.19 ± 0.016 mm/day ($r^2=0.79$, Fig. 5).

We compared the regression lines of standard length on increment count from RES 2 and RES 4 (Fig. 5) using the t-statistic according to Zar (1984) and found no significant difference between the slopes ($t=1.048$; $0.20<P<0.50$). This indicated that the growth rate was not different between the two stations. A common slope for both data sets was computed by using a weighted regression coefficient (Zar, 1984). The resulting combined growth rate for all walleye pollock larvae in Resurrection Bay was 0.18 mm/day.

In addition to length at age (increment count), we examined the relationships between otolith size and increment count and between otolith size and standard length. The regressions of otolith diameter on increment count resulted in a much tighter fit for both stations ($r^2=0.85$ for RES 2 and $r^2=0.91$ for RES 4; Fig. 6). Regressions of length on otolith size indicated a close relationship between body length and otolith diameter for the limited size range studied here ($r^2=0.83$ and $r^2=0.86$).

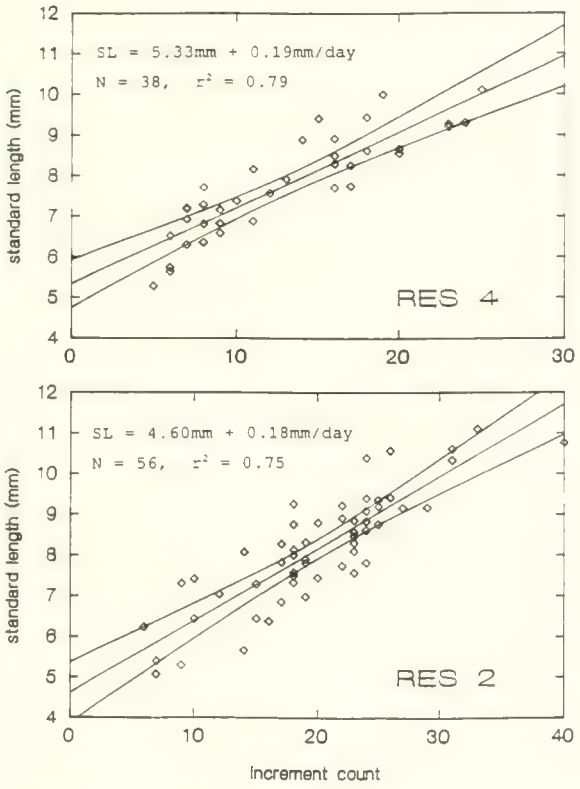

Figure 5

Linear regression of standard length on increment count for otoliths from larval walleye pollock, *Theragra chalcogramma*, at stations RES 2 and RES 4 in Resurrection Bay, Alaska.

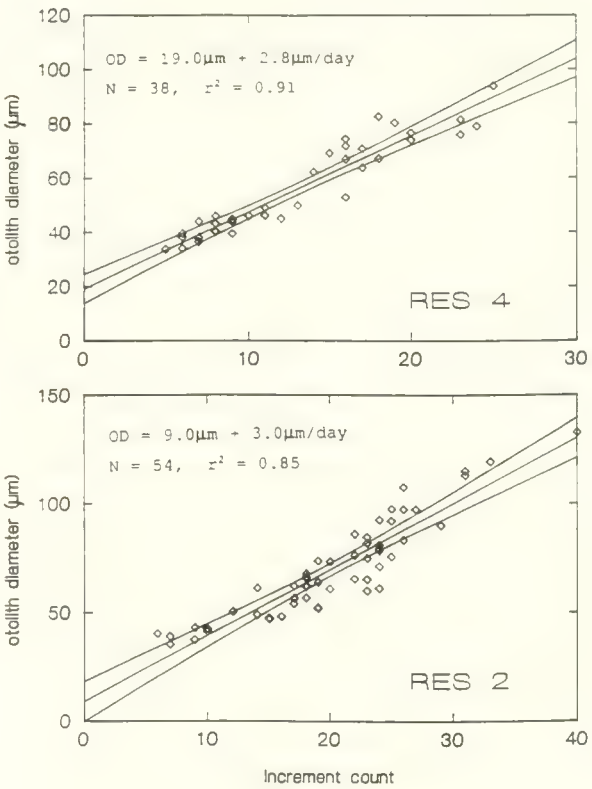

Figure 6

Linear regression of otolith diameter (OD) on increment count for otoliths from larval walleye pollock, *Theragra chalcogramma*, at stations RES 2 and RES 4 in Resurrection Bay, Alaska.

A comparison of elevations (y-intercept) of the two regression lines (Zar, 1984) also resulted in no significant difference (t=1.797; 0.05<P<0.10). Since the two subsamples used for ageing came from different preservatives, no common regression equation was computed. The regression equations relating length and age for larvae preserved in isopropyl alcohol was

$$SL = 4.60 \text{ mm} + 0.18 \text{ mm/day} \times \text{age(days)}.$$

Thus the following equation was used to convert length in isopropyl alcohol to ages:

$$\text{Age} = (SL - 4.60)/0.18.$$

Hatch dates

Estimated hatch dates for all larvae collected 1–4 May 1989 ranged from March 29 to May 9 with a median on 22 April (Fig. 7). Without mortality correction the median hatch date was 25 April.

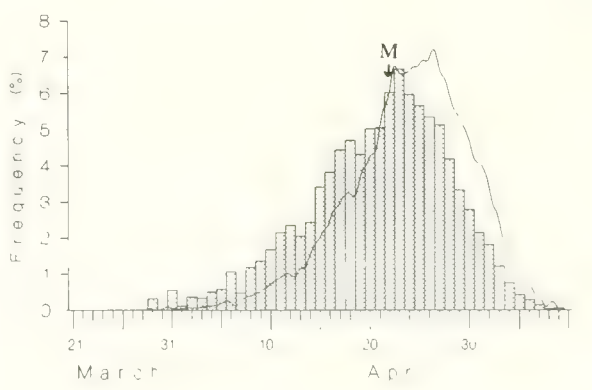

Figure 7

Estimated hatch date distributions of larval walleye pollock, *Theragra chalcogramma*, collected in Resurrection Bay, Alaska, 1–4 May 1989. Solid line shows hatch date distribution without mortality correction. "M" indicates median hatch date for mortality-corrected distribution.

Discussion

Distribution of pollock larvae in relation to hydrography

The vertical distribution of larval walleye pollock is influenced by behavioral responses to gravity, light, thermal stratification, turbidity, and turbulence (Olla and Davis, 1990). Even yolk-sac larvae are capable of oriented vertical movement. Olla and Davis (1990) found that larvae moved away from 3°C water in a vertical temperature gradient. Thus, temperature gradients may be reflected in the vertical distribution of walleye pollock larvae.

The results of this study show that the vertical distribution of walleye pollock larvae differed between the inner and the outer basin of Resurrection Bay in May 1989. Larvae at the outermost stations, RES 4 and GAK 1, were distributed deeper in the water column (Fig. 3). This is consistent with an upward migration of young larvae after hatching. Larvae are significantly younger at the outer stations and are distributed deeper in the water column and closer to the depth of hatching. Alternatively, larvae may select a preferred temperature by avoiding layers of cold water. Water temperatures below 40 m were about 1°C warmer at GAK 1 than at all stations inside the sill (Fig. 2). Temperatures at RES 4, located between GAK 1 and the sill, were intermediate. Cold water of less than 4°C below 40 m in the inner basin might prevent larvae from descending in the water column, resulting in the observed shallow distribution.

The horizontal distribution of larvae is largely determined by upper layer flow. Surface inflow of water into Resurrection Bay has been observed in acoustic doppler current profiler (ADCP) transects across the fjord, and average flow at 15 m depth at a mooring location above the sill was up-fjord between June and October 1989 (Weingartner[2]). If the water in this layer flowed up the fjord during April and May, it would provide a mechanism for advection of larvae into Resurrection Bay. Inflow of water at 15 m requires a compensating outflow. If the upper layer flow is divided in the horizontal plane with inflow on one side of the fjord and outflow on the other side, larvae may simply be transported through the fjord and their residence time could be very short. Alternatively, if surface inflow is compensated for by subsurface outflow or outflow in a shallow low-salinity surface layer, larvae could accumulate inside the fjord if they maintain their vertical position in the water column.

The available evidence suggests that the former mechanism, i.e. two-way surface flow, dominates in the outer fjord basin. The relatively high surface salinity at GAK 1 suggests that the water in the outer basin originates on the shelf. A salinity transect across GAK 1 shows relatively low salinities at both ends of the transect and higher salinities in the center. This does not imply, but is consistent with, an inflow of water along the east side of the outer fjord basin and an outflow along the western shore. Inflow of nearshore water along the eastern shore into Resurrection Bay can be seen in satellite images of the area (Royer[3]) and there is evidence from ADCP transects for a counterclockwise circulation in the outer basin (Weingartner[4]). Larvae that originate on the shelf thus may be carried counterclockwise through the outer basin. Larvae could be carried into the inner fjord by intrusions of surface water across the sill. We probably observed such an intrusion between 1 and 3 May 1989 (Müter, 1992).

It has been demonstrated for several fjords in Norway that water exchange processes can have a profound influence on the community structure within fjords (Lindahl and Perissinotto, 1987). Advective processes can even be the major factor regulating zooplankton biomass in a fjord (Lindahl and Hernroth, 1988). Advection of plankton into Resurrection Bay from the shelf is evidenced by the fact that in addition to resident nearshore species like *Pseudocalanus* spp., oceanic copepods (*Calanus* spp.) common in the Alaska Coastal Current, are found in high concentrations inside the fjord (Smith et al., 1991). Larval walleye pollock found inside Resurrection Bay could similarly originate on the shelf and enter the fjord as a result of advective processes. Plankton samples collected in 1991 suggest that larvae entered the fjord from outside (Müter, unpubl. data). However, acoustic surveys indicated the presence of adult walleye pollock inside Resurrection Bay in the spring of 1983 and at least some spawning may occur inside the fjord (Paul[5]).

Abundance

Our results indicate that walleye pollock larvae were abundant in Resurrection Bay and on the shelf outside Resurrection Bay, as represented by GAK 1. High densities of larval pollock up to 55 larvae·m^{-3} were

[2] Weingartner, T. Institute of Marine Sciences, Univ. Alaska, Fairbanks, AK 99775–1080. Unpubl. data, 1989.

[3] Royer, T. Institute of Marine Sciences, Univ. Alaska, Fairbanks, AK 99775–1080. Personal commun., 1992

[4] Weingartner, T. Institute of Marine Sciences, Univ. Alaska, Fairbanks, AK 99775–1080. Personal commun., 1992.

[5] Paul, A. J. Seward Marine Center, Institute of Marine Sciences, Box 730, Seward, AK. Personal commun., 1992.

also observed in nearby Prince William Sound in May 1989 (Norcross and Frandsen[1]). Larval concentrations inside the fjord in early May 1989 approached those found in the dense larval patch in Shelikof Strait in some years. In most years abundances of early larvae in Shelikof Strait range from 0 to 1,000 larvae·m^{-2} (Kendall et al., 1987; Kendall and Picquelle, 1990), compared with 60–575 larvae·m^{-2} in this study. However, in peak years, abundances in Shelikof Strait exceed the 1989 estimates for Resurrection Bay by one to two orders of magnitude, with 10,000 larvae·m^{-2} in 1981 (Bates and Clark[6]). Larval concentrations in Funka Bay, Japan, decrease from >5,000 larvae·m^{-2} at some stations in January to 200–400 larvae·m^{-2} in early April (Nakatani, 1988). For the Bering Sea, typical abundance estimates range from 10 to 100 larvae·m^{-2} distributed over a very large area (Incze et al., 1984). In Auke Bay, Alaska, the observed abundances were much lower with maximum densities of 3–15 larvae·m^{-2} (Haldorson et al., 1989a).

In ichthyoplankton samples taken in Resurrection Bay in the upper 30 m in 1988, maximum densities ranged from 0.8 larvae·m^{-3} at RES 1 to 4.1 larvae·m^{-3} at RES 4 (Smith et al., 1991), translating into abundances per unit area of 24 larvae·m^{-2} and 124 larvae·m^{-2} respectively. However, these abundances may be underestimates, since only the upper 30 m were sampled by Smith et al. (1991), whereas our study found high abundances below 30 m, particularly in the outer basin of the fjord (Fig. 3). Additional samples were collected in Resurrection Bay in late April and early May 1991. Abundances were similar to those estimated for 1989 (Müter, unpubl. data). The available data from 1988 to 1991 suggest that larval walleye pollock are consistently found in Resurrection Bay. The observed abundances are close to those resulting from the dense spawning aggregations found in Shelikof Strait, Alaska, and Funka Bay, Japan (Kendall and Nakatani, 1992). Since the spatial extent of the spawning area in the vicinity of Resurrection Bay is unknown, total abundances cannot be compared at present.

Larval size and age distribution

Larvae from the shallowest samples at stations RES 1 and RES 2 were significantly larger and older than those at the other stations. Larvae from the shallowest tows may not be representative of the population as a whole because of changes in vertical distribution with age. Thus we also pooled larvae from all tows at each station for between-station comparisons. Some bias may remain because of inconsistencies in the depth sampling regime, but the results were almost identical to those obtained when only shallow samples are used. There is clearly a difference in size and age between larvae at stations RES 1 and RES 2 and larvae at all other stations. This observation is consistent with the hypothesis that larvae are transported into the fjord and accumulate inside the inner fjord basin. A length-frequency distribution for all larvae collected at each station (Fig. 8) shows a multimodal length distribution and

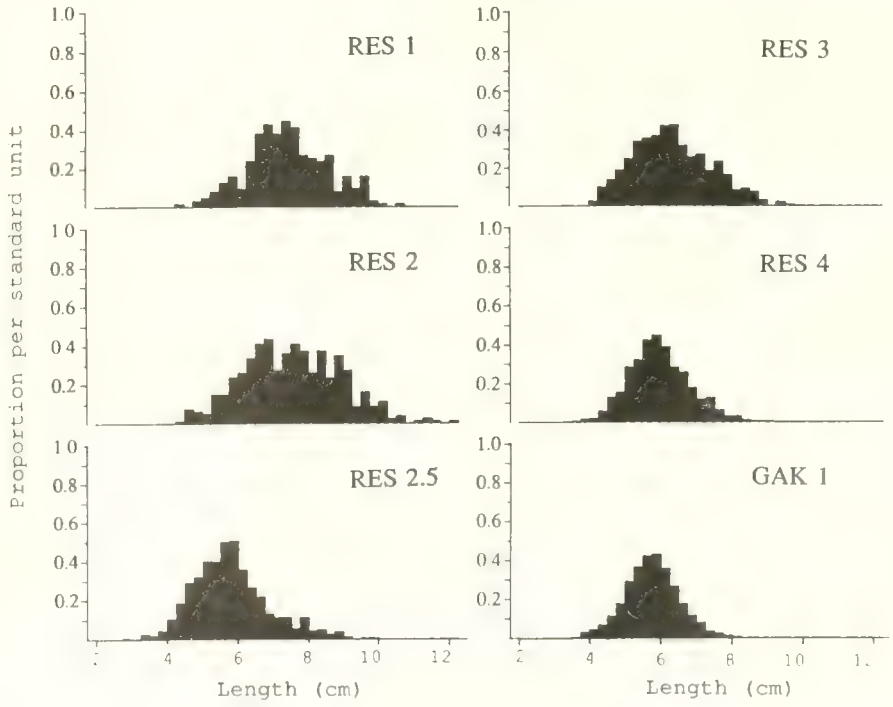

Figure 8

Length-frequency distributions of all larval walleye pollock, *Theragra chalcogramma*, captured at six stations in Resurrection Bay, Alaska, 1–4 May 1989.

[6] Bates, R. D., and J. Clark. 1983. Ichthyoplankton off Kodiak Island and the Alaskan Peninsula during spring 1981. NWAFC Proc. Rep. 83–89. Northwest and Alaska Fisheries Sci. Center, NMFS, NOAA, Seattle, WA, 105 p.

a wide range of measured lengths at both RES 1 and RES 2, whereas at all other stations they show a more narrow, unimodal distribution. This distribution could be the result of several intrusions of surface water and larvae into the inner fjord.

Growth

The growth rates in Resurrection Bay were close to those reported for larvae from other geographic areas (Table 3), including Shelikof Strait and Auke Bay, which are located in the Gulf of Alaska at latitudes similar to Resurrection Bay. Temperatures in the upper layer in Resurrection Bay were slightly lower in early May 1989 than those observed in Shelikof Strait and Auke Bay at the same time of year (Kendall et al., 1987; Pritchett and Haldorson, 1989; Fig. 2). The low temperatures in the inner basin in May reflect delayed warming of the upper water column relative to the shelf outside the fjord. Thus, it may seem that the fjord in early spring provides less favorable conditions for growth than the shelf, considering the lower temperatures inside the fjord. However, salinities also differ between the shelf and the fjord, resulting in a more pronounced stratification inside Resurrection Bay. Stratification of the water column will reduce vertical mixing and can result in an earlier onset of phytoplankton and zooplankton blooms. In spite of differences in temperature, stratification, and vertical distribution (Kim, 1989; Pritchett and Haldorson, 1989), growth rates are very similar in Shelikof Strait, Auke Bay, and Resurrection Bay.

We detected no difference in growth rate between stations RES 2 and RES 4 in Resurrection Bay. This result is not surprising, given the proximity of the stations and the similarity in water properties. The growth rates, especially at the outer station, may be biased because only fish from the shallowest samples were aged. Larvae from the upper layer may not adequately represent the whole population. More samples would be needed to accurately test for differences in growth between stations. To test for interannual differences, data from additional years are needed. Differences in growth rates are most commonly attributed to variations in water temperature and prey concentration. The primary prey of first feeding walleye pollock are copepod nauplii ranging in length from 100 to 300 µm (Kamba, 1977; Clarke, 1978). Smith et al. (1991) found over 20 copepod nauplii (150–350 µm length) per liter throughout May 1988 in Resurrection Bay with numbers exceeding 100 per liter in mid-May. These prey concentrations are sufficient for successful feeding of larval walleye pollock (Paul, 1983; Haldorson et al., 1989b). Under these conditions growth of larvae in Resurrection Bay is not food limited. Growth rates in Resurrection Bay were also similar to those observed in the laboratory under optimal feeding conditions and at a higher temperature (Bailey and Stehr, 1988), further suggesting that growth was not food or temperature limited.

Many studies have documented the effects of water temperature on growth of fish larvae (Houde, 1989). Laboratory studies have shown that first-feeding walleye pollock larvae reared at 5.5°C are more successful at capturing prey than larvae reared at 3°C (Paul, 1983). Brown and Bailey (1992) found geographical differences in growth for juvenile walleye pollock that could be attributed to differences in temperature as well as nutrient levels. In our study, temperatures in the larval environment ranged from 3.5 to 6.3°C and growth rates fall well within the observed range of growth in other habitats.

Hatching and spawning

Hatch dates in Resurrection Bay fall well within the range of observed hatch dates in other parts of the

Table 3

Laboratory and field-estimated growth rates of larval walleye pollock, *Theragra chalcogramma*.

Year	Location	Size range (mm)	Temperature range (°C)	Growth rate (mm day)	Reference
1981	Shelikof Strait	3–13	no data	0.17	Kim and Gunderson (1989)
1983	Shelikof Strait	6–15	5.5–7	0.21	Kendall et al. (1987)
1986	Auke Bay	4–13	6–7	0.23	Haldorson et al. (1989a)
1987	Auke Bay	5–11	5.5–7	0.16	Haldorson et al. (1989a)
1988	Auke Bay	5–11	6–7	0.22	Haldorson et al. (1989a)
1989	Auke Bay	5–12	4–6.5	0.18	Haldorson et al. (1989a)
	Laboratory	4–11	9.3±0.5	0.20	Bailey and Stehr (1986)
	Laboratory	4–10	8–9	0.18	Bailey and Stehr (1988)
	Resurrection Bay	3–15	3.5–6.3	0.18	This study

Table 4

Median hatch dates of larval walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska.

Year	Location	Hatch date	Reference
1983	Shelikof Strait	23 April	Yoklavich and Bailey (1990)
1985	Shelikof Strait	23 April	Yoklavich and Bailey (1990)
1986	Shelikof Strait	29 April	Yoklavich and Bailey (1990)
1987	Shelikof Strait	2 May	Yoklavich and Bailey (1990)
1987	Auke Bay	28 April	Haldorson et al. (1989a)
1989	Resurrection Bay	22 April	This study

Gulf of Alaska (Table 4). The median hatch date is remarkably consistent among different parts of the Gulf and among different years which would require a common, underlying mechanism to trigger spawning over such a broad geographical range. The values from Shelikof Strait suggest a trend towards later spawning dates between 1983 and 1987. More data are needed to determine if a similar trend exists in other areas of the Gulf and to identify parameters responsible for the timing of spawning.

Conclusions

The high abundances and growth rates of larvae in Resurrection Bay indicate that the fjord provides a suitable environment for the successful growth of larval walleye pollock. The hydrography of the region and larval size distributions support the hypothesis that larvae recruit to the fjord from outside by advection into the outer basin of Resurrection Bay and across the sill. These observations and the high abundances of pollock larvae in nearby Prince William Sound during the same year (Norcross and Frandsen[1]) suggest that a large spawning population of walleye pollock exists in the region and that not all walleye pollock in the northern Gulf of Alaska spawn in Shelikof Strait. Larval walleye pollock are also abundant in the bays of Southeast Alaska (Haldorson et al., 1989, a and b). Thus, it is likely that many embayments along the Gulf of Alaska are utilized by this species.

Future work is needed to determine the extent of spawning in the vicinity of Resurrection Bay and Prince William Sound and to test whether the area is consistently used by larval walleye pollock or whether abundances observed in 1989 were unusual. Also, the residence time of larvae in the area is not known. While larval pollock were found in Resurrection Bay in all three years for which data are available, there has been only one report of juvenile walleye pollock in the fjord (Feder et al., 1979).

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Literature cited

Bailey, K. M., and C. L. Stehr.
1986. Laboratory studies on the early life history of the walleye pollock, *Theragra chalcogramma* (Pallas). J. exp. Mar. Biol. Ecol. 99:233–246.
1988. The effects of feeding periodicity and ration on the rate of increment formation in otolith of larval walleye pollock, *Theragra chalcogramma*, Pallas. J. exp. Mar. Biol. Ecol. 122:147–161.

Brown, A.L., and K. M. Bailey.
1992. Otolith analysis of juvenile walleye pollock *Theragra chalcogramma* from the western Gulf of Alaska. Mar. Biol. 112:23–30.

Carmo Lopes, P. do.
1979. Eggs and larvae of *Maurolicus muelleri* (Gonostomatidae) and other fish eggs and larvae from two fjords in western Norway. Sarsia 64:199–210.

Clarke, M. E.
1978. Some aspects of the feeding biology of larval pollock, *Theragra chalcogramma* (Pallas), in the southeastern Bering Sea. M.S. thesis, Univ. of Alaska, Fairbanks, Alaska, 44 p.

De Silva, S. S.
1973. Abundance, structure, growth and origin of inshore clupeid populations of the west coast of Scotland. J. exp. Mar. Biol. Ecol. 12:119–144.

Dunn, J. R., and A. C. Matarese.
1987. A review of the early life history of northeast Pacific gadoid fishes. Fish. Res. 5:163–184.

Feder, H. M., A. J. Paul, and J. McDonald.
1979. A preliminary survey of the benthos of Resurrection Bay and Aialik Bay, Alaska. Sea Grant Report 79-9. Alaska Sea Grant Program, Fairbanks, Alaska, 53 p.

Haldorson, L., A. J. Paul, D. Sterritt, and J. Watts.
1989a. Annual and seasonal variation in growth of larval walleye pollock and flathead sole in a southeastern Alaskan bay. Rapp. P.-v. Reun. Cons. int. Explor. Mer 191:220–225.

Haldorson, L., J. Watts, D. Sterritt, and M. Pritchett.
1989b. Seasonal abundance of larval walleye pollock in Auke Bay, Alaska, relative to physical factors, primary production, and production of zoo-

plankton prey. *In* Alaska Sea Grant Report 89-1, p. 159–172.

Hinckley, S., K. M. Bailey, S. J. Picquelle, J. D. Schumacher, and P. J. Stabeno.
1991. Transport, distribution, and abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. Can. J. Fish. Aquat. Sci. 48:91–98.

Houde, E. D.
1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. 87:471–495.

Incze, L. S., M. E. Clarke, J. J. Goering, T. Nishiyama, and A. J. Paul.
1984. Eggs and larvae of walleye pollock and relationships to the planktonic environment. *In* D. H. Ito (ed.), Proceedings of the workshop on walleye pollock and its ecosystem in the eastern Bering Sea, p. 109–159. NOAA Tech. Memo. NMFS F/NWC-62.

Kamba, M.
1977. Feeding habits and vertical distribution of walleye pollock, *Theragra chalcogramma* (Pallas), in early life stage in Uchiura Bay. Res. Inst. N. Pac. Fish., Hokkaido Univ., Spec. Vol., p. 175–197.

Kendall, A. W., Jr., and S. J. Picquelle.
1990. Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Fish. Bull. 88:133–154.

Kendall, A. W., Jr., and T. Nakatani.
1992. Comparisons of early-life-history characteristics of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska, and Funka Bay, Hokkaido, Japan. Fish. Bull. 90:129–138.

Kendall, A. W., Jr., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert.
1987. Distribution, feeding and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish. Bull. 85:499–521.

Kim, S.
1989. Early life history of walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska. *In* Alaska Sea Grant Report 89-1, p. 117–139.

Kim, S., and D. R. Gunderson.
1989. Cohort dynamics of walleye pollock in Shelikof Strait, Gulf of Alaska, during egg and larval periods. Trans. Am Fish. Soc. 118:264–273.

Lie, U.
1978. Eggs and larvae of fish from Lindaspollene. Sarsia 63(3):163–167.

Lindahl, O., and R. Perissinotto.
1987. Short-term variations in the zooplankton community related to water exchange processes in the Gullmar Fjord, Sweden. J. Plankton Res. 9:1113–1132.

Lindahl, O., and L. Hernroth.
1988. Large-scale and long-term variations in the zooplankton community of the Gullmar Fjord, Sweden, in relation to advective processes. Mar. Ecol. Prog. Ser. 43:161–171.

Lloyd, D. S., and S. K. Davis.
1989. Biological information required for improved management of walleye pollock. *In* Alaska Sea Grant Report 89-1, p. 9–31.

Matthews, J. B. L., and B. R. Heimdal.
1980. Pelagic productivity and food chains in fjord systems. *In* H. J. Freeland, D. M. Farmer, and C. D. Levings (eds.), Fjord oceanography. Plenum Press, New York, p. 377–397.

Megrey, B. A.
1991. Population dynamics and management of walleye pollock *Theragra chalcogramma* in the Gulf of Alaska, 1976–1986. Fish. Res. 11:321–354.

Müter, F. J.
1992. Distribution, abundance, and growth of larval walleye pollock (*Theragra chalcogramma*) in an Alaskan fjord. M.S. thesis, Univ. Alaska Fairbanks, 91 p.

Nakatani, T.
1988. Studies on the early life history of walleye pollock in Funka Bay and vicinity, Hokkaido. Mem. Fac. Fish., Hokkaido Univ. 35:1–46.

Olla, B. L., and M. W. Davis.
1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser. 63:105–112.

Paul, A. J.
1983. Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 13:175–179.

Pritchett, M., and L. Haldorson.
1989. Depth distribution and vertical migration of larval walleye pollock (*Theragra chalcogramma*). *In* Alaska Sea Grant Report 89-1, p. 173–183.

Rogers, D. E., B. J. Rogers, and R. J. Rosenthal.
1987. The nearshore fishes. *In* D. W. Hood and S. T. Zimmerman (eds.), The Gulf of Alaska, physical environment and biological resources. Mineral Management Service OCS study MMS 86-0095, p. 399–416.

Royer, T. C.
1982. Coastal freshwater discharge in the northeast Pacific. J. Geophys. Res. 87:2017–2021.

Schumacher, J. D., and A. W. Kendall Jr.
1991. Some interactions between young walleye pollock and their environment in the western Gulf of Alaska. CalCOFI Rep., Vol. 32, p. 22–40.

Smith, R. L., A. J. Paul, and J. M. Paul.
1991. Timing and abundance of herring and other fish larvae in an Alaskan glaciated fjord. *In* Proc. int. herring symposium Oct. 1990, Anchorage, Alaska. Alaska Sea Grant Report 91-01.

Yoklavich, M. M., and K. M. Bailey.
1990. Hatching period, growth and survival of young walleye pollock *Theragra chalcogramma* as determined from otolith analysis. Mar. Ecol. Prog. Ser. 64:13–23.

Zar, J. H.
1984. Biostatistical analysis. Prentice-Hall, New Jersey, 718 p.

Interannual variation in the recruitment pattern and abundance of age-0 summer flounder, *Paralichthys dentatus*, in Virginia estuaries*

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Abstract.—Capture of transforming larval and newly settled juvenile (age-0) summer flounder, *Paralichthys dentatus*, over four years (1986–1989) in the seaside salt marshes of Virginia's Eastern Shore and in the lower Chesapeake Bay verifies Virginia waters as a nursery area. Gear specific for juvenile flatfish was used and sampling was conducted in a broad range of habitats in all months. This study demonstrates a fluctuation in the timing of the appearance and magnitude of abundance of age-0 summer flounder in Virginia waters over a four-year sampling period. Age-0 summer flounder (11–27 mm TL) began entering the area in October 1986 and were present throughout the winter of 1987. The 1988 and 1989 year classes did not appear until April at larger sizes (22–83 mm TL). Highest catch per unit of effort (CPUE) occurred between April and August and abundance declined in the fall. Data indicated that year-class strength declined from 1986 to 1988 and increased slightly in 1989. To monitor year-class strength of age-0 summer flounder, we recommend sampling Virginia estuaries in April, May, and June when both abundance of flounder is high and small-mesh-lined trawl gear is most efficient.

Summer flounder, *Paralichthys dentatus* (Pleuronectiformes: Bothidae), is an important commercial and recreational species along the eastern coast of the United States. It ranges from Nova Scotia (Scott and Scott, 1988) to Florida (Gutherz, 1967) and its center of abundance occurs in the Middle Atlantic Bight (Scarlett, 1981). Though it is known that commercial landings of *P. dentatus* in the Middle Atlantic Bight fluctuate widely (Wilk et al., 1980), fluctuations in abundance of age-0 summer flounder have not been investigated. Because of the economic importance of summer flounder in Virginia, our first objective was to design a sampling plan based on the early life history of summer flounder to assess the relative yearly abundance of age-0 summer flounder in Virginia waters. This index will provide the fishing industry and fishery managers with knowledge of fluctuations before those fluctuations affect the fishery. A part of designing an effective sampling plan was evaluation of appropriate gear. Therefore, the second objective was to examine the effectiveness of sampling gear.

Age-0 *P. dentatus* have been captured in small numbers from Chesapeake Bay (Orth and Heck, 1980; Weinstein and Brooks, 1983) and the Eastern Shore of Virginia (Richards and Castagna, 1970). Poole (1966) hypothesized that Virginia waters and the sounds of North Carolina constitute primary nursery areas for summer flounder, but an insufficient number of specimens have been captured to substantiate this hypothesis. Recruitment and distribution patterns of age-0 summer flounder have been investigated in estuaries in North Carolina (Powell and Schwartz, 1977; Miller et al., 1984; Burke et al., 1991)

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and New Jersey (Able et al., 1990); however, the studies in Virginia reporting the capture of age-0 summer flounder were not directed specifically at this species (Richards and Castagna, 1970; Orth and Heck, 1980; Weinstein and Brooks, 1983). Thus the third objective of this study was to assess the region's importance as a nursery area.

Methods

Sampling sites were located on the seaside (eastern border) and bayside (western border) of Virginia's Eastern Shore and on the western shore of Chesapeake Bay (Fig. 1) because the Chesapeake Bay and Eastern Shore were hypothesized to be prime nursery grounds (Poole, 1966). The eastern border of the Eastern Shore peninsula is an extensive system of barrier islands enclosing salt marshes and shallow bays that are 1–2 m deep at mean high water (MHW). The bays and salt marshes are transected by main channels that are 3–20 m deep at MHW. On the western border of the peninsula, there are shallow creeks, 1–6 m deep at MHW, which extend into upland areas. Fringing and pocket marshes, much less extensive than the seaside salt marshes, occur along creek margins. Seagrass beds are present at the mouth of most creeks. The mouth of the York River (Fig. 1) is 3.7 km wide; it has extensive shoal areas along its margins and a main channel 18 m deep. Salt marshes, with channels 1–3 m deep, and seagrass beds are present in the shoal areas.

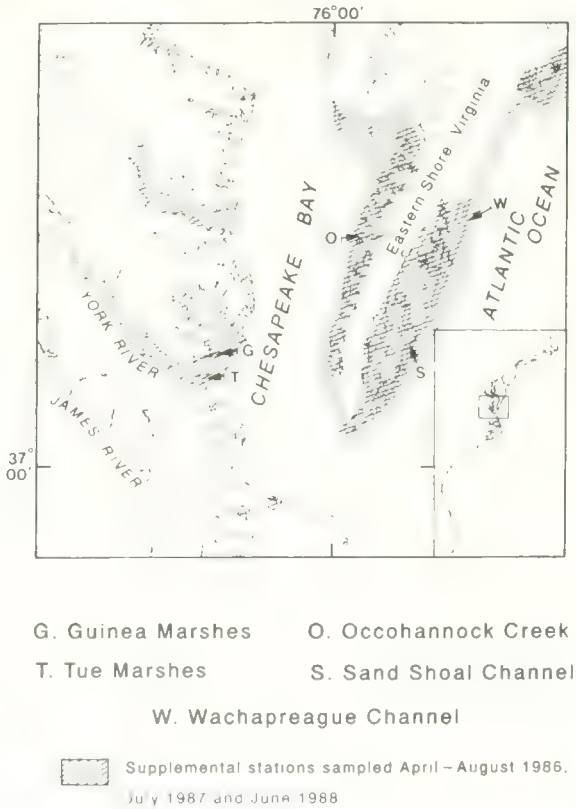

Figure 1

Locations of sampling sites for *Paralichthys dentatus* on Virginia's Eastern Shore and in Chesapeake Bay and its tributaries. Letters indicate sites with regular, fixed station sampling; shading indicates areas in which rivers, creeks, and nearshore locations were sampled during 1986 preliminary investigations and supplemental investigations in July 1987 and June 1988.

Between 1986 and 1989, three different types of 4.9-m semi-balloon otter trawls with 19.1-mm bar mesh in the wings and upper body were used to sample areas 1–11 m in depth. Only bar mesh sizes are noted in this paper. The first unlined trawl, used in 1986 and July 1987, had 6.4-mm mesh in the lower body and codend. We added a 3.2-mm mesh liner to the codend in September to capture the newly settled juveniles. Because ctenophores and jellyfish could clog the mesh, mesh sizes of the unlined trawl were increased to 19.1 mm in the lower body and to 15.9 mm in the codend in August 1987. To compare the sampling efficiency of the lined and unlined trawls, both trawls were towed at each station from September 1987 onward. All trawls were fished with a 4.8-mm link tickler chain to increase catches of flatfish (see Creutzberg et al., 1987).

Two 6.1-mm seines were used to sample shallow (<1 m) habitats. A beach seine (6.4-mm mesh) was used in April and May 1986 and a bag seine (3.2-mm mesh) was used from November 1986 until December 1988. A 3.2-mm link chain was attached to the leadline of both seines to increase catches of flatfish.

Trawling and seining were conducted from April 1986 to August 1989 during daylight hours (Norcross and Hata, 1990). While designing the study from April to August 1986, sampling was conducted at least once in most navigable waters of the Eastern Shore and at the mouth of the York River (Fig. 1). Over the next two years, September 1986–September 1988, samples were collected at fixed stations at five sites (Fig. 1): Wachapreague and Sand Shoal Channels, Occohannock Creek, and Guinea and Tue Marshes (also see Wyanski, 1990). At each site, deep (5–11 m) water stations were located in the middle of channels, whereas shallow (<5 m) water stations were situated along channel margins. All stations had sand or fine-grained substrates. Samples were collected semi-monthly from September 1986 through

August 1987, and at monthly intervals thereafter. During expected periods of peak age-0 summer flounder abundance in 1987 and 1988, additional samples were collected throughout the study area (Fig. 1).

Sampling was reduced spatially and further reduced temporally in 1989. Sampling was eliminated at Occohannock Creek, the site at which the fewest number of summer flounder were captured. Sampling was conducted April through August at the other four sites. Only trawling was continued.

We measured the total length (TL) of each summer flounder and used the length-frequency data to identify age-0 individuals. A birthdate of 1 January (Smith et al., 1981) was used when designating year class, although age-0 summer flounder may have been collected the preceding October through December. For each gear, data from all sampling efforts were pooled by month and by year class and catch per unit of effort (CPUE) was calculated as the mean number of age-0 summer flounder per 15-m seine haul or 5 minutes of trawl sample. To make sample sizes more similar among the treatment groups (year class) in statistical analyses, the 15-month time period over which a year class was sampled was separated into two time intervals: October–June and September–December. July and August data were not included in analyses because of bias produced by the clogging of meshes.

Some data were eliminated from statistical analyses owing to changes in the gear. Only seine data for the 1987 and 1988 year classes were compared because a different seine was used in 1986. Unlined trawl data for the 1986 year class were eliminated because the mesh size was smaller than in subsequent years. Because of nonrandom (fixed) station locations and nonindependent samples, nonparametric statistical tests were used to analyze the CPUE data. For each gear, the Mann-Whitney test or Kruskal-Wallis test was used to compare monthly CPUE values among years (Zar, 1984). If the null hypothesis in the Kruskal-Wallis test was rejected, a multiple comparison test (Dunn, 1964) was used to determine which means were significantly different. If P was <0.05, the results were considered significant.

Results

We were able to identify the age-0 year class for 15 months (October through December of the next year) using length frequencies from all four years of data combined (Fig. 2). Table 1 shows the application of these monthly size-at-age criteria to identify the age-0 specimens in individual years. Sizes ranged from 11 mm to the largest age-0 specimen of 285 mm. Little to no change in mean size was observed from October to May, whereas rapid size changes were apparent from June to September.

Though sampling effort and gear varied among years, age-0 summer flounder were caught within Virginia waters in each year of the study. Over the four years of sampling, age-0 *P. dentatus* were captured each month but not during every month of every year (Table 2). Summer flounder exhibited a prolonged period of recruitment to inshore waters as age-0 specimens were captured in Virginia estuaries from October to May (Table 2, Fig. 2). Newly settled specimens (<20 mm) were collected throughout the fall and winter of 1986–87; however, they were not collected in the fall and winter of 1987–88 and 1988–89. When age-0 specimens first appeared in April of 1988 and 1989, they were already >20 mm.

The highest CPUE values were reported for April through September (Table 2). Comparisons of CPUE

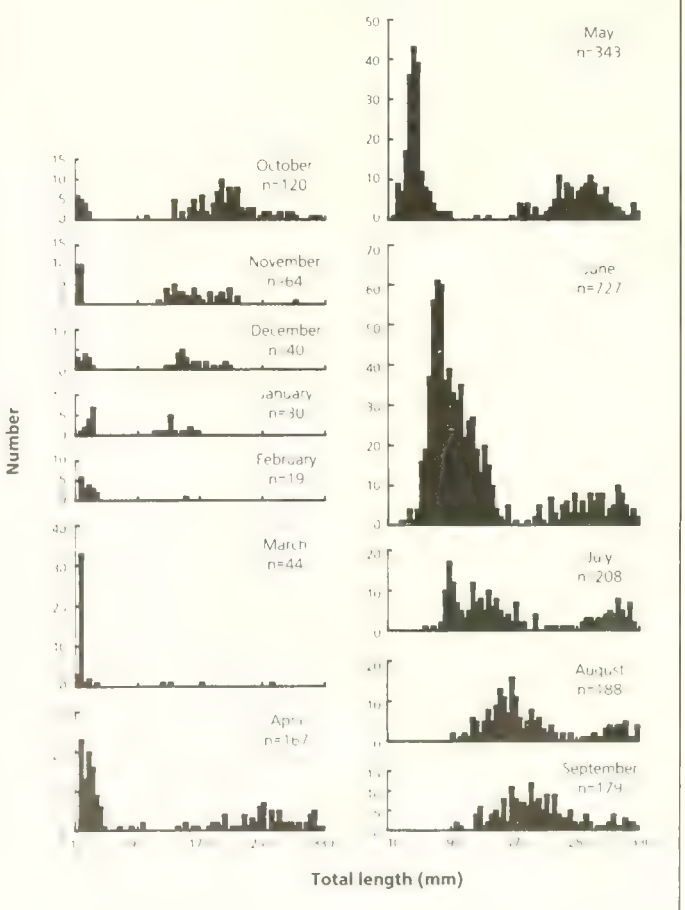

Figure 2

Combined monthly length frequencies of age-0 and age-1 *Paralichthys dentatus* in Virginia captured at all sites shown in Figure 1 from 1986 through 1989.

Table 1

Length ranges (mm) of age-0 summer flounder, *Paralichthys dentatus*, from all sites by year class for 15 months.

	1986 Year class	1987 Year class	1988 Year class	1989 Year class
Oct	—	11–27	—	—
Nov	—	13–19	—	—
Dec	—	14–32	—	—
Jan	—	17–34	—	—
Feb	—	17–38	—	—
Mar	—	14–27	—	—
Apr	26–69	15–48	22–83	36–41
May	22–60	21–80	24–32	17–88
Jun	54–140	27–160	35–160	35–144
Jul	96–190	68–180	86–180	57–160
Aug	30–220	93–240	115–210	90–210
Sep	96–265	147–275	176–222	—
Oct	100–285	170–265	172–245	—
Nov	119–218	—	—	—
Dec	131–185	168–209	—	—

data pooled over the five sampling sites for each of the three gear types showed a general pattern of reduced age-0 summer flounder abundance in Virginia estuaries between 1986 and 1988; there was a slight increase in 1989, based on trawl data (Table 3). The CPUE of the seine and the unlined trawl decreased an order of magnitude per year from 1986 to 1988.

Twice as many summer flounder (101 vs. 54) were captured in seven seine hauls in April and May 1986 as in 527 seine hauls over the next two years (Table 3). For October–June data, CPUE in seine hauls was significantly greater in 1987 than in 1988 (Table 4) as no *P. dentatus* were captured in 1988. Seining, though successful in 1986, did not yield many age-0 flounder in 1987–1988 (Tables 2 and 3), and thus was discontinued.

The unlined trawl data revealed no significant differences in CPUE between years (Table 4). We did not include 1986 unlined trawl data in analyses, but the high CPUE values for this gear type in May and June provided additional evidence that abundance was greater in 1986 compared with 1987–1989.

The lined trawl data for October–June revealed significant differences in CPUE among years (Table

Table 2

Catch per unit of effort (CPUE) of age-0 summer flounder, *Paralichthys dentatus*, by year class for 15 months from all sites. Seine CPUE = number of age-0 flounder 15 m haul; trawl CPUE = number of age-0 flounder/5 min; — = no of sample taken.

	1986 year class (1985-86)			1987 year class (1986–87)			1988 year class (1987–88)			1989 year class (1988-89)		
		Trawl			Trawl			Trawl			Trawl	
Month	Seine	Lined[1]	Unlined[2]	Seine[3]	Lined	Unlined	Seine[3]	Lined[1]	Unlined[4]	Seine	Lined[1]	Unlined[4]
Oct	—	—	—	—	0.03	—	0	0	0	0	0	0
Nov	—	—	—	0.08	0.36	—	0	0	0	0	0	0
Dec	—	—	—	0.24	0.16	—	0	0	0	0	0	0
Jan	—	—	—	0.13	0.14	—	0	0	0	—	—	—
Feb	—	—	—	0.13	0.21	—	0	0	0	—	—	—
Mar	—	—	—	0.29	0.50	—	0	0	0	—	—	—
Apr	16.60[5]	—	—	0.79	0.75	—	0	0.05	0	—	0.06	0
May	9.00[5]	—	13.81	0.33	1.51	—	0	0.13	0	—	1.14	0.29
Jun	—	—	4.08	0.04	3.98	—	0	0.06	0.06	—	3.27	2.00
Jul	—	—	2.01	0.17	3.84	1.38	0	0.14	0.18	—	1.88	2.00
Aug	—	—	3.70	0.08	—	0.96[4]	0	0.26	0.37	—	0.71	1.28
Sep	—	0.87	—	0	0.29	0.65[4]	0	0.22	0.61	—	—	—
Oct	—	0.69	—	0	0.42	1.65[4]	0	0.35	0.43	—	—	—
Nov	0[3]	0.56	—	0	0	1.00[4]	0	0.13	0	—	—	—
Dec	0[4]	0.31	—	0	0	0.17[4]	0	0	0	—	—	—

[1] Semi balloon otter trawl (3.2-mm mesh liner).
[2] Semi balloon otter trawl (6.4-mm mesh).
[3] Bag seine (3.2-mm mesh).
[4] Semi balloon otter trawl (15.9-mm mesh).
[5] Bag seine (6.4-mm mesh).

4); CPUE was higher in 1987 than in 1988. No other differences were detected. For September–December data, there were no significant differences in CPUE among the 1986, 1987, and 1988 year classes (Table 4).

Gear efficiency changed as fish size increased. The unlined trawl with 15.9-mm mesh in the codend produced generally lower CPUE values than the lined trawl during April through June (Table 2). As the age-0 specimens increased in size, the CPUE values for the unlined trawl became higher than those for the lined trawl.

Discussion

The prolonged time of age-0 summer flounder recruitment to the inshore waters of Virginia is more extended than entry times for North Carolina waters where age-0 *P. dentatus* enter estuaries from December through April (Deubler, 1958), January through April (Burke et al., 1991), or February through April (Warlen and Burke, 1990). October through May recruitment to Virginia also agrees with reports of transforming larvae of *P. dentatus* (≤20 mm TL) entering New Jersey inlets from October through May (Able et al., 1990). Age-0 summer flounder were not collected from October through May during all years of our study. They may appear in the fall or winter but often are not evident until April. Similar variation in timing of and size at first collection was reported in New Jersey, where age-0 flounder (<50 mm) were collected in the fall and during May but only occasionally during the winter months (Able et al., 1990). Thus, appearance of summer flounder in Virginia estuaries seems to be more similar to that of New Jersey (fall and late spring) rather than to that seen in North Carolina (winter and early spring). The time of first entrance in New Jersey, Virginia, and North Carolina estuaries corresponds with spawning periods of September–December north, and November–

Table 3

Summary of collection data from all sites by year class for age-0 *Paralichthys dentatus*: number of 15-m seine hauls, number of age-0 flounder captured, seine catch per unit of effort (CPUE) = number of age-0 flounder/haul, number of trawl tows, total minutes tow time for lined and unlined trawls, number age-0 flounder captured, trawl CPUE = number of flounder/5 min tow.

	Year class			
	1986	1987	1988	1989
Seine				
Number of hauls	46	295	232	0
Number of flounder	108	54	0	0
CPUE	1.20	0.18	0.00	—
Lined Trawl				
Number of tows	282	739	320	93
Number of minutes	1410.0	3664.5	1578.5	426.0
Number of flounder	192	670	30	96
CPUE	0.68	0.91	0.10	1.13
Unlined Trawl				
Number of tows	125	206	334	94
Number of minutes	613.8	1015.5	1657.8	467.0
Number of flounder	436	192	33	97
CPUE	3.55	0.94	0.10	1.04

Table 4

Summary of statistical tests used to compare catch per unit of effort (CPUE) for *Paralichthys dentatus* between years for various gear and time intervals. H_0 = the null hypothesis; U = Mann-Whitney (MW) statistic; H = Kruskal-Wallis (KW) statistic; Q = multiple comparison statistic (Dunn, 1964); df = degrees of freedom; * = significant results at 0.05 level of significance.

Gear	Months	H_0	Statistic	P	Test
Seine	Oct–Jun	1987=1988	U=72	<0.001	MW
Unlined trawl	Oct–Jun	1988=1989	U=34	>0.20	MW
Unlined trawl	Sep–Dec	1987=1988	U=14	0.10<P<0.20	MW
Lined trawl	Oct–Jun	1987=1988=1989	H=10.310* df=2	0.005<P<0.01	KW
		1987=1988	Q=3.22*	0.002<P<0.005	MC (D)
		1987=1989	Q=1.64	0.2<P<0.5	MC (D)
		1988=1989	Q=1.21	P>0.5	MC (D)
Lined trawl	Sep–Dec	1986=1987=1988	H=5.734 df=2	0.05<P<0.10	KW

February south, of Chesapeake Bay as suggested by Smith (1973).

There are several possible explanations for the interannual differences in timing of recruitment to the inshore waters and size at first collection: 1) abundance is so low in some years that age-0 fish are not encountered; 2) newly settled summer flounder are utilizing habitats that were not sampled; and 3) summer flounder juveniles do not enter estuaries at the same time and size in all years.

The first explanation seems plausible for the 1988 year class which apparently had no October 1987–March 1988 recruitment and extremely low numbers in summer (Table 2). However, there also was no October–March recruitment in 1988–89, yet abundance indices in May–August 1989 were comparable to those in 1987, a year with October–May recruitment. We sampled a limited number of fixed sampling sites, thus in years of relatively low abundance, an uneven distribution of the fish would appear as though recruitment did not occur.

Newly settled summer flounder may be utilizing certain habitats which were not sampled because of location or gear accessibility. Habitats, such as eelgrass beds, would be difficult to sample with trawl and seine gear (Able et al., 1990) and therefore the flounder would be unavailable to the gear. Newly recruiting summer flounder are most abundant in marsh creeks in New Jersery (Szedlmayer et al., 1992). In some years of our study, the flounder could have been present in eelgrass beds or marsh creeks that we did not sample. From our data, it would then appear as if winter recruitment had not taken place.

Recruitment of summer flounder juveniles may not be represented by a characteristic place, time, and size of fish. Able et al. (1990) suggested that some juveniles utilize the continental shelf as a nursery and thus enter estuaries at a larger size. This could explain the apparent lack of fall/winter recruitment that we observed in the 1988 and 1989 year classes. Variability in time of recruitment to inshore waters of Virginia observed over the three years of fall/winter sampling in this study is analogous to that in New Jersey waters. Newly recruiting summer flounder were collected in southern New Jersey estuaries from November 1988 through May 1989, but no summer flounder juveniles were collected in the corresponding months of 1987 and 1988 (Szedlmayer et al., 1992).

Variation of year-class strength in fish populations has been a topic of investigation since it was first proposed by Hjort (1914), but fluctuations in year-class strength must be identified before causes of the variation can be investigated. Four years of sampling did not provide sufficient data to define a "normal" level of recruitment; however, it appears that there was relatively poor recruitment of age-0 summer flounder to Virginia waters in 1988 compared with 1986, 1987, and 1989 (Tables 2 and 3), suggesting that there was large interannual recruitment variability. This decrease in year-class strength was verified by catches of age-1 summer flounder in Chesapeake Bay and nearshore coastal waters one year later (Desfosse et al.[1]). The highest CPUE values for the seine and trawls occurred in spring 1986, suggesting that the 1986 year class was possibly the strongest of the four year classes. Given the larger mesh size in the seine and unlined trawl in spring 1986, these high CPUE values are probably underestimates when compared with CPUE values for the seine and lined trawl in 1987–89.

We cannot speculate what effect poor year-class strength of summer flounder will have on the fishery two to four years later because it is not known what percentage of the fishable population is dependent on Virginia nursery areas. If Virginia waters are a primary nursery area, the impact to the fishery could be great. Because our data and those of Desfosse et al.[1] documented poor year classes in 1987–89, the Virginia Marine Resources Commission (VMRC) closed the nearshore (<3 miles) trawl fishery for summer flounder effective 1 July 1989 (Travelstead[2]) as a precautionary measure to protect those year classes.

Estimation of summer flounder juvenile recruitment is biased by small-scale distribution patterns, mesh size, and gear performance under certain conditions. Gear efficiency changes with size of fish. The 3.2- and 6.4-mm mesh seines and trawls used in our study captured smaller specimens in the winter and spring than did the 15.9-mm mesh trawl, but these gear become less efficient with increasing fish size, probably due to increased gear avoidance. Despite similar mesh sizes, the sampling effectiveness of the bag seine decreased more rapidly than did the lined trawl, probably because of the movement of age-0 summer flounder to deeper habitats at 60–80 mm TL (see Wyanski, 1990). No age-0 summer flounder were captured by seine later than August. We agree with Williams and Deubler (1968) that environmental factors, such as current velocity and mechanical clogging of nets, can also have a pronounced effect on sampling success for flounder. We found that gear efficiencies depend on season (e.g. density of jellyfish) and size of flounder.

[1] Desfosse, J. C., J. A. Musick, A. D. Estes, and P. Lyons. 1989. Stock identification of summer flounder (*Paralichthys dentatus*) in the southern Mid-Atlantic Bight. Virginia Inst. Mar. Sci., Gloucester Point, VA 23062. Ann. Prog. Rep. WB-86-01-03.

[2] Travelstead, J. VMRC, Newport News, Virginia 23607. Personal commun., June 1989.

To develop an index to monitor interannual variation in year-class strength of summer flounder, we suggest sampling in Virginia estuaries during April, May, and June with a small mesh (e.g. 3.2 mm) lined beam trawl. Beam trawls (Kuipers, 1975; Kuipers et al., 1992) have been found to be more effective at capturing flatfishes than have otter trawls (Gunderson and Ellis, 1986) which were used in this study. We recommend using a beam trawl with tickler chains to increase catch, particularly on sand or fine-grained sediment. Diver observations and catch comparisons of flatfishes by beam and otter trawls in Alaskan waters (Norcross, unpubl. data) support this recommendation.

Though summer flounder can be captured through October (Fig. 2), the fish are larger but fewer from July to October. This pattern of increasing densities during the period of settlement, followed by a continuous decrease has also been observed in plaice (*Pleuronectes platessa*) in the North Sea (Veer et al., 1990). Thus we recommend sampling during the period of increasing densities, because later in the season low numbers of captured individuals reduce the sensitivity of the catch data to reflect year-class strength.

Data presented here support the hypothesis of Poole (1966) that Virginia waters are a nursery ground for summer flounder. Variation in CPUE during the four years of our study makes it difficult to conclude that this area is a "primary" nursery during all years.

In addition to Virginia, summer flounder use areas in New Jersey (Szedlmayer et al., 1992), Delaware (Malloy and Targett, 1991) and North Carolina (Burke et al., 1991) as nursery grounds. The same sample gear and strategy need to be used throughout the range of summer flounder (New Jersey to North Carolina) to compare the relative importance of specific locations as nursery areas. A multi-year study combined with sampling over a finer spatial scale would allow interannual variation in primary nursery locations to be determined.

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Literature cited

Able, K. W., R. E. Matheson, W. W. Morse, M. P. Fahay, and G. Shepard.
1990. Patterns of summer flounder *Paralichthys dentatus* early life history in the Mid-Atlantic Bight and New Jersey estuaries. Fish. Bull. 88:1–12.

Burke, J. S., J. M. Miller, and D. E. Hoss.
1991. Immigration and settlement pattern of *Paralichthys dentatus* and *P. lethostigma* in an estuarine nursery ground, North Carolina, U.S.A. Neth. J. Sea Res. 27:393–405.

Creutzberg, F., G. C. A. Duineveld, and G. J. van Noort.
1987. The effect of different numbers of tickler chains on beam-trawl catches. J. Cons. int. Explor. Mer 43:159–168.

Deubler, E. E.
1958. A comparative study of the postlarvae of three flounders (*Paralichthys*) in North Carolina. Copeia 1958:112–116.

Dunn, O. J.
1964. Multiple contrasts using rank sums. Technometrics 6:241–252.

Gunderson, D. R., and I. E. Ellis.
1986. Development of a plumb staff beam trawl for sampling demersal fauna. Fish. Res. 4:35–41.

Gutherz, E. J.
1967. Field guide to the flatfishes of the family Bothidae in the western North Atlantic. U.S. Fish Wildl. Serv., Circ. 263, 47 p.

Hjort, J.
1914. Fluctuations in the great fisheries of northern Europe. Rapp. P.-v. Reun. Cons. int. Explor. Mer 20:1–13.

Kuipers, B. R.
1975. On the efficiency of a two metre beam trawl in juvenile plaice (*Pleuronectes platessa*). Neth. J. Sea Res. 9:69–85.

Kuipers, B. R., B. MacCurrin, J. M. Miller, H. W. van der Veer, and J. IJ. Witte.
1992. Small trawls in juvenile flatfish research: their development and efficiency. Neth. J. Sea Res. 29:109–117.

Malloy, K. D., and T. E. Targett.
1991. Feeding, growth and survival of juvenile summer flounder *Paralichthys dentatus*: experimental analysis of the effects of temperature and salinity. Mar. Ecol. Prog. Ser. 72:213–223.

Miller, J. M., J. P. Reed, and L. J. Pietrafesa.
1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. *In* J. D. McCleave, G. P.

Arnold, J. J. Dodson, and W. H. Neill (eds.), Mechanisms of migration in fishes, p. 209–225. Plenum Publ. Corp.

Norcross, B. L., and D. Hata.
1990. Seasonal composition of finfish in waters behind the Virginia barrier islands. Va. J. Sci. 41:441–461.

Orth, R. J., and K. L. Heck Jr.
1980. Structural components of eelgrass (*Zostera marina*) meadows in the lower Chesapeake Bayfishes. Estuaries 3:278–288.

Poole, J. C.
1966. A review of research concerning summer flounder and needs for further study. N.Y. Fish Game J. 13:226–231.

Powell, A. B., and F. J. Schwartz.
1977. Distribution of paralichthid flounders (Bothidae: *Paralichthys*) in North Carolina estuaries. Chesapeake Sci. 18:334–339.

Richards, C. E., and M. Castagna.
1970. Marine fishes of Virginia's eastern shore (inlet and marsh, seaside waters). Chesapeake Sci. 11:235–248.

Scarlett, P. G.
1981. Fishery management plan for the summer flounder (*Paralichthys dentatus*) fishery. Atl. States Mar. Fish. Comm., Fish. Manage. Rep. 3, 80 p.

Scott, W. B., and M. G. Scott.
1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219, 731 p.

Smith, W. G.
1973. The distribution of summer flounder, *Paralichthys dentatus*, eggs and larvae on the continental shelf between Cape Cod and Cape Lookout, 1965–66. Fish. Bull. 71:527–548.

Smith, R. W., L. M. Dery, P. G. Scarlett, and A. Jearld Jr.
1981. Proceedings of the summer flounder (*Paralichthys dentatus*) age and growth workshop, 20–21 May 1980, Northeast Fisheries Center, Woods Hole, Massachusetts. NOAA Tech. Memo., NMFS-F/NEC-11, 30 p.

Szedlmayer, S. T., K. W. Able, and R. A. Roundtree.
1992. Growth and temperature-induced mortality of young-of-the-year summer flounder (*Paralichthys dentatus*) in southern New Jersey. Copeia 1992:120–128.

Veer, H. W. van der, L. Pihl, and M. J. Bergman.
1990. Recruitment mechanisms in North Sea plaice *Pleuronectes platessa*. Mar. Ecol. Prog. Ser. 64:1–12.

Warlen, S. M., and J. S. Burke.
1990. Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. Estuaries 13:453–461.

Weinstein, M. P., and H. A. Brooks.
1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. Mar. Ecol. Prog. Ser. 12:15–27.

Wilk, S. J., W. G. Smith, D. E. Ralph, and J. Sibunka.
1980. Population structure of summer flounder between New York and Florida based on linear discriminant analysis. Trans. Am. Fish. Soc. 109:265–271.

Williams, A. B., and E. E. Deubler Jr.
1968. A ten year study of macroplankton in North Carolina estuaries: assessment of environmental factors and sampling success among bothid flounders and penaeid shrimps. Chesapeake Sci. 9:27–41.

Wyanski, D. M.
1990. Patterns of habitat utilization in 0-age summer flounder (*Paralichthys dentatus*). M.A. thesis, College of William and Mary, 54 p.

Zar, J. H.
1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 718 p.

Spatio-temporal structure of the deep-water shrimp *Aristeus antennatus* (Decapoda: Aristeidae) population in the western Mediterranean

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Abstract.—The spatio-temporal structure of a population of the deep-water shrimp *Aristeus antennatus* on the fishing grounds off Barcelona, Spain, in the western Mediterranean Sea was studied, and the relationship between fluctuations in catch of this species and spatio-temporal changes in the size and sex composition of shoals is described. Fluctuations were monitored by using a sample design based on fixed seasonal sampling of three different habitats (upper submarine canyon, middle slope, and lower slope). The results explain changes in fishing fleet and fishing location. The stock appears to remain constant at approximately optimum levels of exploitation because part of it is unexploited below 1,000 m.

Factorial correspondence analysis indicated a generally strong influence of depth on the abundance of deep-water shrimp, explaining 63.14% of the variance. However, the influence of seasonality was stronger when only samples taken at depths shallower than 1,000 m (75.22%) were considered. Females contributed most to the catches on the upper and middle slope throughout the year, and catches of females were strongly related to seasonality ($P<0.05$). The combined interaction of depth and seasonality on the abundance of males was significant ($P<0.05$). Juveniles were present in the catches from autumn to spring, and the combined effect of depth and seasonality on the abundance of juveniles was also significant ($P<0.05$). The role of the regional submarine canyon as a zone of higher energy and biomass in the recruitment of this species is discussed, and the importance of spatio-temporal factors linked to the life cycle of deep-water shrimps is highlighted. The results demonstrate that comprehensive ecological studies of exploited species are essential to proper fisheries management.

As fishing activity has expanded into deeper waters, deep-water shrimps (Dendrobranchiata and Caridea) have become an important resource in different parts of the world, e.g. Australia (King, 1981; King and Butler, 1985) northern Europe (Anon., 1992), and the Pacific (Gooding, 1984) and Indian (Jones, 1969) oceans. In the Mediterranean Sea in particular, these shrimps are the target of a traditional fishery (Relini and Orsi Relini, 1987; Tobar and Sardà, 1987; Campillo et al., 1990; Demestre, 1990; Demestre and Lleonart, 1993). In addition, deep-water shrimps, particularly aristeid species (Dendrobranchiata, Penaeoidea: *Aristeus antennatus* Risso, 1816), play an important ecological role in Mediterranean deep-sea communities at depths below 400 m (Pérès, 1985; Abelló et al., 1988; Abelló and Valladares, 1988; Cartes and Sardà, 1993). Population structure, biological cycles, life history, and spawning strategies of deep-water shrimps differ from those of littoral species (García and Le Reste, 1987) and are poorly understood. The life history of deep-water penaeoidean species is not dependent upon lagoonal or littoral systems, and growth in such species tends to be slower than that in littoral penaeid species (García and Le Reste, 1987; Demestre, 1990). The presence and abundance of such species are linked to the topography of the continental slope and submarine canyons. However, their behavioral patterns are complex and not well understood (Tobar and Sardà, 1987; Cartes et al., 1993).

Pandalus borealis (Anon., 1992) (Pandalidae, Caridea) is the most extensively studied shrimp species from a fisheries perspective. This species exhibits major differences with respect to species of other genera inhabiting subtropical deep-sea regions, such as *Aristeus*, *Aristaeomorpha*, *Parapandalus*, and *Plesionika*; it is protandrously hermaphroditic and distributed in shallower waters. Migratory patterns, short and medium-term fluctuations in abundance, aggregating behavior, recruitment, and larval and postlarval dis-

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tribution patterns are to a large extent still unknown in deep-water species of the latter genera.

Moreover, recently published data on the distribution and abundance of deep-water shrimps in the western Mediterranean (*Aristeus antennatus*, *Acanthephyra eximia*, *Nematocarcinus exilis*) indicate relatively high biomass levels for these species at depths down to 2,200 m (Abelló and Valladares, 1988; Cartes and Sardà, 1992, 1993; Sardà and Cartes, 1993a). Fishing pressure in shallow waters has resulted in a shift of effort to deeper regions, making the study of deepwater species extremely important, while exploitation of these resources is still low (King, 1981; Demestre, 1990; Demestre and Lleonart, 1993). Growth, reproductive biology and morphometry of *Aristeus antennatus* in particular has been studied by several authors (e.g. Bas, 1965; Relini Orsi and Relini, 1979; Arrobas and Ribeiro-Cascalho, 1987; Sardà and Demestre, 1987; Demestre and Fortuño, 1992; Sardà et al., in press). In contrast, the only available information on population structure (sex-ratio, size distribution, proportion of juveniles) and spatio-temporal migrations has been compiled from commercial fisheries data (Relini and Orsi Relini, 1987; Tobar and Sardà, 1987, 1992).

The objective of the present study is to examine the relationship between fisheries exploitation and the distribution and spatio-temporal structure of a population of *A. antennatus* in the three different habitats occupied by this species: submarine canyons on the upper slope, the middle slope, and lower slope. The study attempts to integrate our basic knowledge of the biology and population structure of this species with the pattern of fishing activity in the region. We provide a basis for interpreting catch fluctuations observed during the year and for managing this fishery consistent with the general ecology of the species.

Materials and methods

Sampling was designed to survey spatio-temporal features in two different habitats (one station in each) where commercial catches of *A. antennatus* were common: the submarine canyon known as "La Merenguera" located on the upper slope (US) at a depth of approximately 450 m (41°07'75"N, 02°04'43"E) and the area known as the "Abisinia" fishing grounds on the middle slope (MS) at a depth of 600–650 m (41°06'34"N, 02°12'05"E). A third station was located on the upper portion of the lower slope (LS) at a depth of about 1,200 m (41°54'63"N, 02°06'90"E), where no fishing activity takes place (Fig. 1). Habitat nomenclature follows Pérès (1985). Three replicate tows were carried out within a period of less than 12 hours at each sampling station in summer, autumn, winter, and spring (Table 1). The trawl gear was a "Maireta system" (Spanish patent: 9200614, Inst. Ciencias del Mar [CSIC], consisting of a semi-balloon otter trawl with square panels and wings and a 25-m headline. The gear was towed by a single warp line attached to a V-shaped backstrop, which was in turn connected to two 450-kg iron doors. The horizontal gear opening (the wing-end spread of 14 m) was measured by using a SCANMAR system. Codend stretch mesh size was 2 mm (Sardà et al., 1993). Trawls were conducted by the Research Ship *García del Cid*.

Towing speed was 2.5 knots for all trawls. Starting and ending positions of each tow were recorded by using a GPS system. Specimens of *A. antennatus* were weighed and sexed (M=males; F=females), and short carapace length (CL) in mm was measured (rear edge of ocular orbit to rear edge of carapace). Male and female individuals smaller than 23 mm CL were classified as juveniles (J) (Sardà and Demestre, 1987; Demestre, 1990). Smaller individuals (CL <15 mm) were uncommon in the samples; such

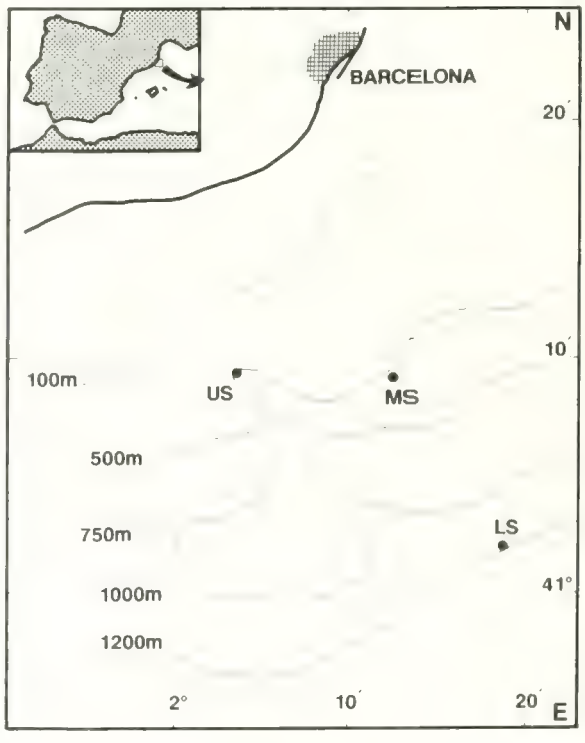

Figure 1

Map of the study area showing the location of sampling stations. US=upper slope; MS=middle slope; LS=lower slope (see text for explanation).

individuals were considered to represent the early juvenile stages (L) and were analyzed separately to obtain information on the earliest stages of recruitment.

Spatio-temporal changes in population structure were analyzed by using factorial correspondence analysis (FCA) (Benzecri, 1980; Greenacre, 1984). Data were logarithmically transformed and a data matrix was constructed by using the three habitats sampled and the following variables: number of males (M), number of females (F), number of juveniles (J), number of smaller juveniles (L), and total number. Because the LS below 1,000 m is a stable habitat that, unlike the US and MS, is less affected by seasonal factors (Hopkins, 1984; Tyler, 1988; Gage and Tyler, 1991) and is not exploited by the fishery (Demestre, 1986; Sardà and Martín, 1986), the analysis was repeated excluding samples taken on the LS (Table 2).

Multifactorial nonparametric analysis of variance (Zar, 1984) was used to calculate differences between variable and habitat combinations in each season (spring, summer, fall, and winter). The Mood nonparametric median test (Conover, 1980) was also used to determine differences in total number of individuals by habitat.

Table 1

Sample list and specific haul data for collections of rose shrimp, *Aristeus antennatus*. P=spring; W= winter; A=autumn, and S=summer. US=upper slope; MS=middle slope, and LS=lower slope.

Ref. code	Season	Habitat	Date	Haul time (h)	Mean depth (m)
R1/1	P	MS	04/23/91	1.00	570
R1/2	P	MS	04/23/91	1.50	600
R1/3	P	MS	04/23/91	1.67	692
R1/4	P	US	04/23/91	1.00	455
R1/5	P	US	04/23/91	1.00	459
R1/6	P	US	04/23/91	1.00	390
R1/7	P	LS	04/25/91	1.00	1160
R1/8	P	LS	04/25/91	1.00	1210
R1/9	P	LS	04/25/91	1.00	1230
R2/7	A	MS	12/09/91	1.00	625
R2/8	A	MS	12/09/91	1.00	613
R2/9	A	MS	12/09/91	2.00	562
R2/1	A	US	12/08/91	0.42	433
R2/2	A	US	12/08/91	0.50	455
R2/3	A	US	12/08/91	0.50	504
R2/4	A	LS	12/08/91	1.00	1265
R2/5	A	LS	12/09/91	1.00	1274
R2/6	A	LS	12/09/91	0.50	1252
R3/1	W	MS	03/12/92	0.83	565
R3/2	W	MS	03/12/92	0.75	545
R3/3	W	MS	03/12/92	0.75	545
R3/4	W	US	03/12/92	0.50	355
R3/5	W	US	03/12/92	0.50	447
R3/6	W	US	03/12/92	0.50	508
R3/7	W	LS	03/13/92	1.00	1235
R3/8	W	LS	03/13/92	1.00	1275
R3/9	W	LS	03/13/92	1.00	1210
R4/1	S	MS	07/26/92	1.00	605
R4/2	S	MS	07/26/92	1.00	611
R4/3	S	MS	07/26/92	1.00	616
R4/4	S	US	07/26/92	0.50	426
R4/5	S	US	07/26/92	0.42	400
R4/6	S	US	07/26/92	0.50	440
R4/7	S	LS	07/27/92	1.00	1260
R4/8	S	LS	07/27/92	1.00	1286
R4/9	S	LS	07/27/92	1.00	1272

Results

The first two inertial axes of the correspondence analysis explained 63.14% and 26.84% of the variance in abundance of shrimp, respectively (Fig. 2). Along the first axis, LS samples were associated with a higher proportion of males and early juvenile stages (L), which did not exhibit any marked seasonal pattern in the deepest region. However, the samples collected in summer on both the US and MS were mainly females and were located in the region opposite the LS samples (Fig. 2). In summary, the first axis was mainly related to depth and juveniles predominated in the US and MS samples collected in spring, autumn, and winter.

The results of the analysis, excluding samples taken on the LS (Fig. 3), yielded a cluster of data points for spring samples associated with the presence of juveniles (recruits); in contrast, data points for summer samples were again associated with adult females. Autumn and winter samples were less clearly discriminated but shifted to the right from the origin and were associated with males. This may be interpreted as a seasonal effect that alters the population structure and is discriminated by the first axis, which explained 75.22% of the total variance (Fig. 3A). The distribution of juveniles appeared to be linked to the topography of the submarine canyons (black points in Fig. 3B), mainly during winter and spring, while the proportion of males rose on the middle slope out to the canyon in autumn and winter (open symbols, Fig. 3B). Juveniles and early juvenile stages (L) were caught in the deepest region sampled (Table 2 and Fig. 2). In summer females were distributed extensively on both the MS and the US. In this second analysis the first axis may be related to seasonality. The second axis (20.27%) probably represents a depth-related component, because the samples from the MS were taken at slightly greater depths (600–650 m) than those taken from the US (400–500 m).

Table 2

Basic data matrix in number of individuals per sample of *Aristeus antennatus:* M=males; F=females; J=juveniles (CL<23 mm); L=early juvenile stages (CL<15 mm); *n*=total number; US=upper slope; MS=middle slope; LS=lower slope. P=spring; A=autumn; W=winter and S=summer, (—)=no data.

		US			MS			LS		
Replicates		1	2	3	1	2	3	1	2	3
	M	74	15	48	153	51	31	—	39	19
	F	359	113	298	178	314	132	—	21	15
P	J	241	60	166	198	86	73	—	40	24
	L	0	0	0	0	0	0	—	0	0
	n	433	128	346	331	265	163	—	60	34
	M	40	82	44	7	5	4	11	24	36
	F	160	378	166	5	8	17	14	11	14
A	J	112	160	94	8	5	4	19	29	42
	L	0	0	0	0	0	0	1	0	0
	n	200	460	160	12	13	21	25	35	50
	M	0	12	6	130	11	24	4	26	25
	F	0	62	42	212	30	107	3	15	12
W	J	0	32	32	102	11	20	4	23	22
	L	0	0	0	0	0	0	0	3	3
	n	0	74	48	342	41	131	7	41	37
	M	18	12	0	0	4	0	63	51	353
	F	820	144	166	53	104	196	45	14	120
S	J	52	30	4	41	5	5	65	40	285
	L	0	0	0	0	0	0	4	2	6
	n	838	156	166	53	108	196	108	65	473

Seasonal groupings of samples revealed significant differences in the analysis of variance (Table 3). When the deepest station (LS) was included in the analysis, the total number of individuals were significantly different with depth ($P<0.05$). This variation with depth can be explained by the fact that, on average, fewer individuals were collected at the station on the LS ($P<0.01$) (Fig. 4).

Differences in the number of females were also significantly related to depth ($P<0.05$); females were more abundant at shallower stations on the MS and US. Males collected from the three habitats exhibited significant differences for interaction between depth and seasonality ($P<0.05$) (Table 3), which resulted from the higher percentage of males on the LS all year and on the MS in autumn and winter.

When the deepest samples (LS) were excluded, differences between the number of males and the total number of individuals were significant between seasons ($P<0.05$) and for the interaction between depth and season ($P<0.05$).

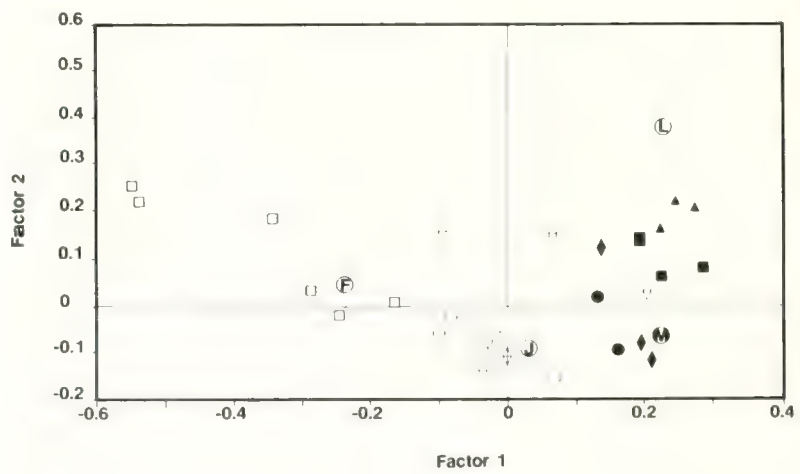

Figure 2

Plots of scores on the first two correspondence axes for the entire set of samples of rose shrimp, *Aristeus antennatus*. F=females; M=males; J=juveniles; L=early juvenile stages; circle=spring; square=summer; triangle=autumn; diamond=winter.

Discussion

The distribution of *A. antennatus* extended to a depth of more than 2,200 m. The population structure in

the deeper region between 1,000 and 2,200 m consisted of a higher proportion of juveniles and males (Cartes and Sardà, 1992; Sardà and Cartes, 1993b; Cartes, in press). This contrasts with the high proportion of females collected at depths of less than 1,000 m.

The present results support the hypothesis that two different populations of *A. antennatus* persist in the western Mediterranean. One population is unexploited and stable throughout the year at depths below 1,000 m and is characterized by lower densities and higher percentages of males and juveniles. The other population is commercially exploited and variable over the year at shallower depths between 400 and 1,000 m. It is characterized by high abundance and by seasonal variations in total number, sex ratio, and depth distribution.

The *A. antennatus* stock, though subjected to considerable fishing pressure, has remained at near optimum equilibrium levels (Demestre and Lleonart, 1993). Sardà (1993) and Sardà and Cartes (1993a) attributed this equilibrium to the presence of unexploited biomass at depths below 1,000 m, which annually renews the exploited portion of the stock.

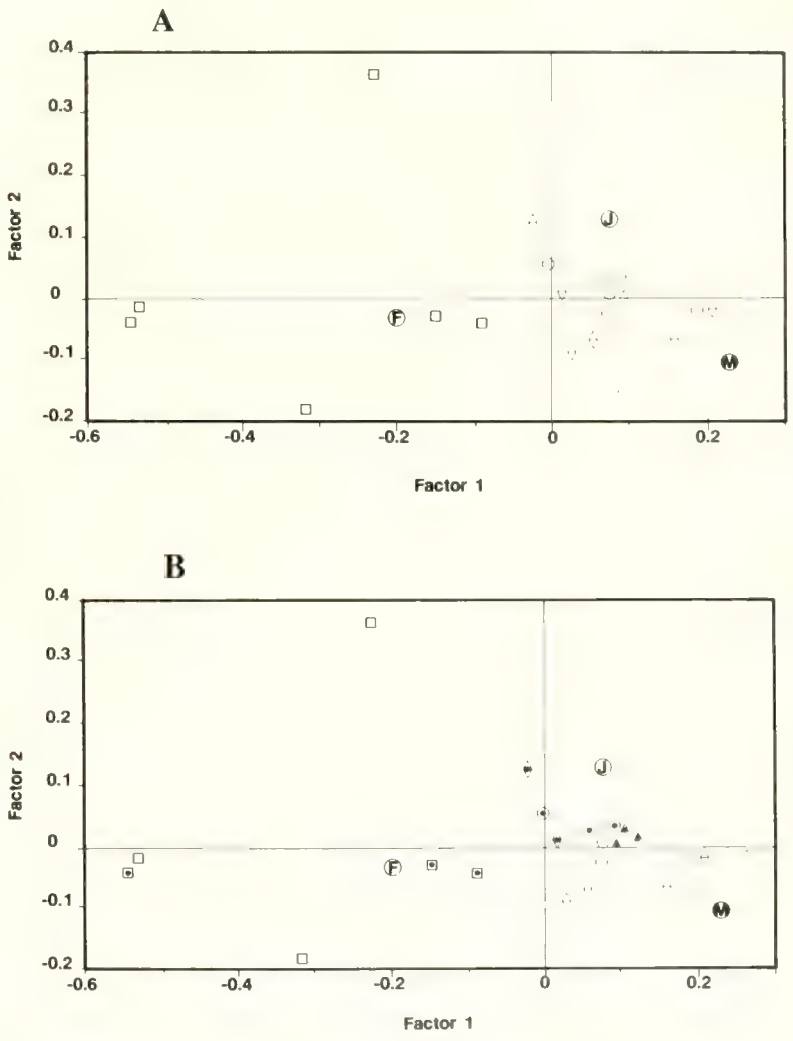

Figure 3

Plots of scores on the first two correspondence axes (**A**) and (**B**) for the entire set of samples of rose shrimp, *Aristeus antennatus* collected on the upper slope (US) and middle slope (MS) only. F=females; M=males; J=juveniles; circle=spring; square=summer; triangle=autumn; diamond=winter. Black points (•) represent canyon samples on upper slope (US).

Though sampling was localized and did not cover extensive areas of each habitat, the samples from the US and MS nonetheless reflected specific spatio-temporal patterns in population structure: females completely dominated the population all year, forming aggregations on the MS in spring and summer. Earlier studies on fishing patterns during the year (Figure 5A, revised after Tobar and Sardà, 1987) have referred to this population migration pattern. Changes in the coefficient of variation of catch rate illustrated in Figure 5B reflect a scattering of the shoals in spring and summer (from April to August) and a more highly aggregated stock structure in autumn and winter. Figure 6 summarizes our conclusions regarding the distribution and movement of *A. antennatus*.

The increase in number of females on the MS in spring and summer coincides with the period of gonadal ripening and fertilization (Relini Orsi and Relini, 1979; Arrobas and Ribeiro-Cascalho, 1987; Sardà and Demestre, 1987; Demestre and Fortuño, 1992) and shortening of the male rostrum (Sardà and Demestre, 1989). These authors also reported that shoals disperse after spawning, which occurs mainly from June to September. This might suggest a specific mating area in the MS. After September, shrimps spread out over the slope and submarine canyons, leading to a decrease in density and increase in the proportion of males on the slope. Processes linked to the transfer of energy through the slope and submarine canyon systems (Reyss, 1971, 1973; or Rowe, 1971;

Koslow and Ota, 1981; Houston and Haedrich, 1984), and feeding habits (Cartes and Sardà, 1989; Cartes, 1991) may also be related to distribution of *A. antennatus*. Ghidalia and Bourgois (1961) and Bombace (1975) associated certain shrimp species with water masses that were of a characteristic septentrional type, with a low temperature of 12.8°C and high salinity (38.1–38.8 ppt). However, it has not been possible to confirm these hydrographic hypotheses for *A. antennatus*, because the study by Ghidalia and Bourgois (1961) reported few catch data of this species. No other studies on related species have established more specific hypotheses.

The growth, abundance, parent stock biomass, and recruitment of commercial species are important when calculating parameters directly related to their population dynamics and exploitation (Caddy and Sharp, 1988; Sardà, 1993). Size-frequency data for *A. antennatus* caught by commercial fishing vessels (Demestre, 1990; Fig. 7) do not show progressions in monthly length-frequency modes. Apparent "negative growth rates" between different months suggest that vessels were following a moving stock and that catches were taken at the most commercially profitable locations. Procedures for analyzing this type of stock have been considered by Jones (1984), Caddy (1982, 1987), and Caddy and García (1986) from fishery catches. Procedures for treating migratory stocks have been considered primarily by Sousa (1988) in the fish *Decapterus russelli*. Bias in size frequencies due to migratory effects in *D. russelli* is similar to

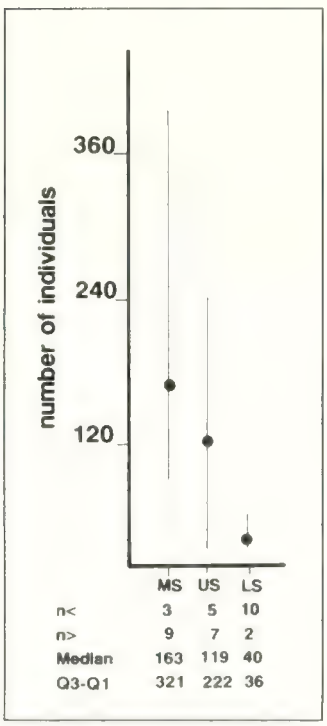

Figure 4

Mean number of individuals of rose shrimp, *Aristeus antennatus*, showing 95% confidence intervals (χ^2=8.67; P< 0.01): '*n*<' =number of samples below median; '*n*>'=number of samples above median; Q3-Q1= difference between maximum and minimum value. US=upper slope; MS=middle slope; LS=lower slope.

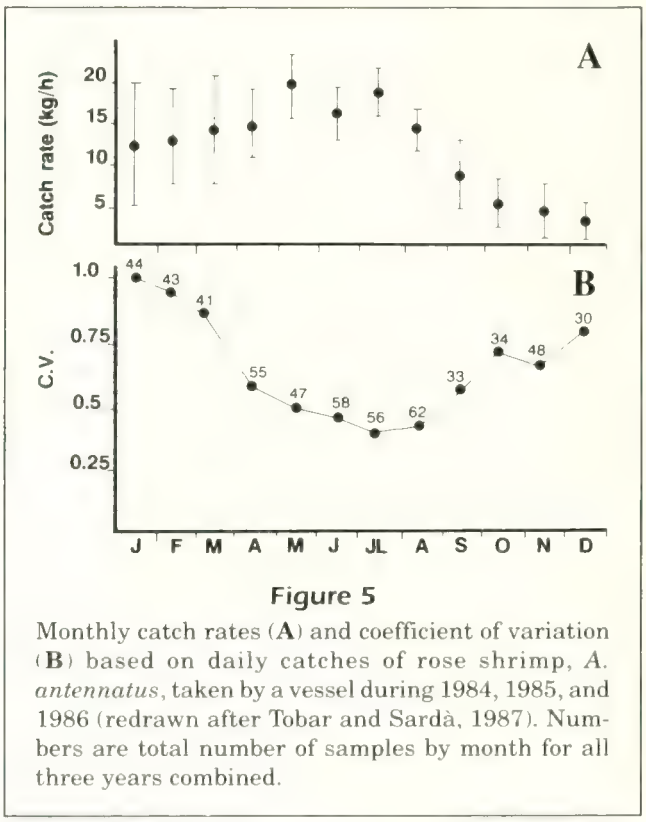

Figure 5

Monthly catch rates (**A**) and coefficient of variation (**B**) based on daily catches of rose shrimp, *A. antennatus*, taken by a vessel during 1984, 1985, and 1986 (redrawn after Tobar and Sardà, 1987). Numbers are total number of samples by month for all three years combined.

Table 3

Results of applying multifactorial nonparametric analysis of variance to the basic data matrix presented in Table 2 for collections of rose shrimp, *Aristeus antennatus*, with and without lower slope (LS) data. M = males; F = females; J=juveniles, *n*=total number; (+)=significant difference (P<0.05); (—)=nonsignificant difference.

	With LS data				Without LS data			
	M	F	J	*n*	M	F	J	*n*
Seasonality	+	—	—	+	—	—	—	—
Depth	—	—	—	—	—	+	—	+
Interaction	+	—	—	+	+	—	+	—

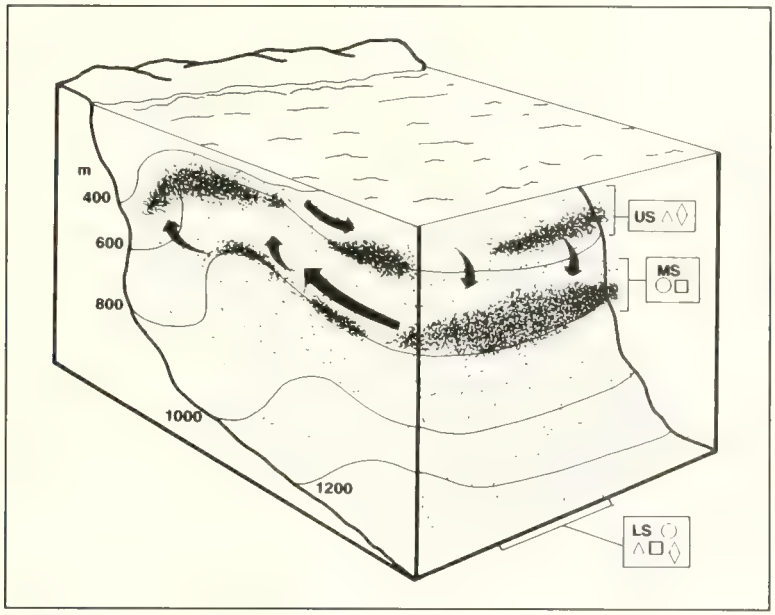

Figure 6

Conceptual model of the spatio-temporal dynamics of *Aristeus antennatus* in the study area (see text for more details). MS=middle slope; US=upper slope, and LS=lower slope; circle=spring; square=summer; triangle=autumn; diamond=winter.

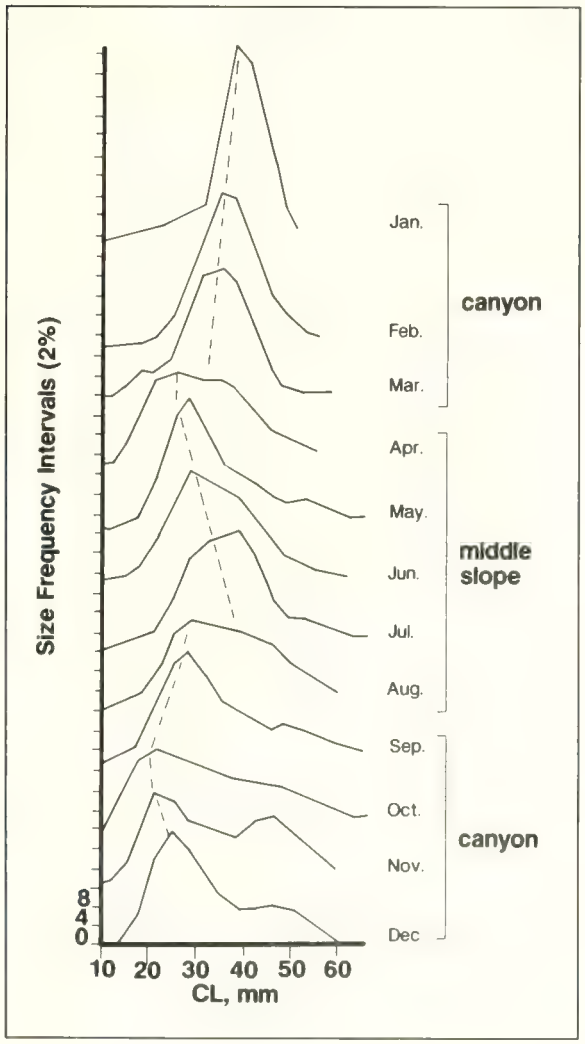

Figure 7

Monthly size frequencies for rose shrimp, *Aristeus antennatus* (carapace length) taken in commercial catches from the upper slope (US) and middle slope (MS) (data from Demestre, 1990).

that observed for *A. antennatus*. Size-frequency modes were evident in spring and summer but did not progress in autumn and winter (Fig. 6). Sparre et al. (1989) advised using the annual-return matched sample method to estimate growth parameters in such cases. Failing to take these aspects into account when considering a population exploited by a given fleet in a given area may lead to errors in calculating biological parameters and, consequently, in decision-making for fishery management.

Acknowledgments

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Literature cited

Anonymous.
1992. Working group on *Nephrops* and *Pandalus* stocks. ICES. CM. 1992/Assess. 8:1–275.

Abelló, P., and F. J. Valladares.
1988. Bathyal decapod crustaceans of the Catalan Sea (northwestern Mediterranean). Mésogée 48:47–102.

Abelló, P., F. J. Valladares, and A. Castellón.
1988. Analysis of the structure of decapod crustacean assemblages off Catalan coast (North-West Mediterranean). Mar. Biol. 98:39–49.

Arrobas, I., and A. Ribeiro-Cascalho.
1987. On the biology and fishery of *Aristeus antennatus* (Risso, 1816) in the South Portuguese coast. Inv. Pesq. 51 suppl. 1:233–244.

Bas, C.
1965. La gamba rosada (*Aristeus antennatus*). Publicaciones Técnicas de la Junta de Estudios de Pesca 5:143–155.

Benzecri, J. P.
1980. L' analyse des données. 2: L'analyse des correspondences. Ed. Dunod, Paris, 632 p.

Bombace, G.
1975. Considerazione sulla distribuzione delle populazione di livello batiale con particulare referimento a quelle bentonectoniche. Pubbl. Zool. Napoli, 39, suppl. 1:7–21.

Caddy, J. F.
1982. Some considerations relevant to the definition of shared stocks and their allocation between adjacent economic zones. FAO Fish. Circ. 749:1–44.
1987. Size-frequency analysis for crustacea: moult increment and frequency models for stock assessment. Kuwait Bull. Mar. Sci. 9:43–61.

Caddy, J. F., and S. García.
1986. Fisheries thematic mapping—a prerequisite for intelligent management and development of fisheries. Oceanogr. Trop. 21(1):31–52.

Caddy, J. F., and G. D. Sharp.
1988. Un marco ecológico para la investigación pesquera. FAO. Doc. Téc. Pesca 283:1–155.

Campillo, A., P. Y. Dremiere, B. Liorzou, and J. L. Bigot.
1990. Observations sur deux crustacés profonds du Golfe du Lyon: *Aristeus antennatus* (R.) et *Nephrops norvegicus* (L.). FAO. Rap. sur les Pêches 447:298–313.

Cartes, J. E.
1991. Analisis de las comunicdades y estructura trofica de crustaceos decapodos. Ph.D. diss., Universidad de Barcelona, 627 p.
In press. Influence of depth and seasonality on the diet of the deep-water aristeid *Aristeus antennatus* along the slope (between 400–2,300 m) in the Catalan Sea (western Mediterranean). Mar. Biol.

Cartes, J. E., and F. Sardà.
1989. Feeding ecology of the deep-water aristeid crustacean *Aristeus antennatus*. Mar. Ecol. Prog. Ser. 54:229–238.
1992. Abundance and diversity of decapod crustaceans in the deep Catalan Sea (western Mediterranean). J. Nat. Hist. U.K. 26:1305–1323.
1993. Zonation of the deep-sea decapod fauna in the Catalan Sea (western Mediterranean). Mar. Ecol. Prog. Ser. 94:27–34.

Cartes, J. E., F. Sardà, J. B. Company, and J. Lleonart.
1993. Day-light migrations by deep-sea decapod crustaceans in experimental sampling in the western Mediterranean. J. exp. Mar. Biol. Ecol. 171:63–73.

Conover, W. J.
1980. Practical non-parametric statistics, 2nd ed. John Wiley & Sons, New York, 493 p.

Demestre, M.
1986. Les diferents comunitats naturals de la Méditerranée. *In* J. Lleonart (ed.), L'Oceanografía, recursos pesquers de la mar Catalana. Quad. Ecol. Aplicada. Diputació de Barcelona (9):9–41.
1990. Biología pesquera de la gamba *Aristeus antennatus* (Risso, 1816) en el mar Catalán. Ph.D. diss., Univ. Barcelona, 443 p.

Demestre, M., and J. M. Fortuño.
1992. Reproduction of the deep-water shrimp *Aristeus antennatus* (Decapoda: Dendrobranchiata). Mar. Ecol. Prog. Ser. 84:41–51.

Demestre, M., and J. Lleonart.
1993. The population dynamics of *Aristeus antennatus* (Decapoda: Dendrobranchiata) in the northwestern Mediterranean. Sci. Mar. 57(2–3):183–189.

Gage, J. D., and P. A. Tyler.
1991. Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge Univ. Press, London, 503 p.

García, S., and L. Le Reste.
1987. Ciclos vitales, dinámica, explotación y ordenación de las poblaciones de camarones peneidos costeros. FAO Doc. Tec. Pesca 203:1–180.

Ghidalia, W., and F. Bourgois.
1961. Influence de la témperature et de l'éclairement sur la distribution des crevettes des moyennes et grandes profondeurs. Stud. Rev. Gen. Fish. Count. Medit., FAO 16:1–53.

Gooding, R. M.
1984. Trapping surveys for the deep-water caridean shrimps *Heterocarpus laevigatus* and *H. ensifer* in the western Hawaiian Islands. Mar. Fish. Rev. 46(2):18–26.

Greenacre, M. J.
1984. Theory and applications of correspondence analysis. Academic Press, London, 364 p.

Houston, K. A., and R. L. Haedrich.
1984. Abundance and biomass of macrobenthos in the vicinity of Carson Submarine Canyon, northwest Atlantic Ocean. Mar. Biol. 82:301-305.

Hopkins, T. S.
1984. Physics of the sea. *In* R. Margalef (ed.), Western Mediterranean. Pergamon Press, Oxford, 363 p.

Jones, R.
1984. Assessing the effects of changes in exploitation using length composition data (with notes on VPA and cohort analysis). FAO Fish. Tech. Pap. 256:0–118.

Jones, S.
1969. The prawns fishery resources of India. FAO Fish. Rep. 57(3):725–748.

King, M. G.
1981. Increasing interest in the tropical Pacific's deep-water shrimps. Aust. Fish. 40(6):33–41.

King, M. G., and A. J. Butler.
1985. Relationship of life-history patterns to depth in deep-water caridean shrimps (Crustacea: Natantia). Mar. Biol. 86:129–138.

Koslow, J. A., and A. Ota.
1981. The ecology of vertical migrations in the three common zooplankters in the La Jolla Bight, April–August 1967. Biol. Oceaonogr. 1:107–134.

Pérès, J. M.
1985. History of the Mediterranean biota and the colonization of the depths. *In* R. Margalef (ed.), Western Mediterranean. Pergamon Press, New York, p. 198–232.

Relini Orsi, L., and J. Relini.
1979. Pesca e riproduzione del gambero rosso *Aristeus antennatus* (Decapoda, Penaeoidae) nel Mar Ligure. Quad. Civica Staz. Idrobiol. Milano 7:1–39.

Relini, G., and L. Orsi Relini.
1987. The decline of red shrimp stocks in the Gulf of Genoa. Inv. Pesq. 51 (supl. 1): 245–260.

Reyss, D.
1971. Les canyons sous-marins de la mer Catalane: le rech du Cap et le rech Lacaze-Duthiers. III: Les peuplements de macrofaune benthique. Vie et Milieu 22:529–613.
1973. Les canyons sous-marins de la mer Catalane: le rech du Cap et le rech Lacaze-Duthiers. IV: Etude synécologyque des peuplements de macrofaune benthique. Vie et Milieu 23:101–142.

Risso, A.
1816. Historie naturelle des Crustacés des environs de Nice, 175 p.

Rowe, G. T.
1971. Observations on bottom currents and epibenthic populations in Hatteras Submarine Canyon. Deep-Sea Res. 18:569–581.

Sardà, F.
1993. Bio-ecological aspects of the fisheries of Crustacea Decapoda in the western Mediterranean. Aquat. Living Resour. 6:299–305.

Sardà, F., and J. E. Cartes.
1993a. Distribution, abundance and selected biological aspects of *Aristeus antennatus* in deep-water habitats in NW Mediterranean. B.I.O.S. (Thessaloniky, Greece) 1(1):59–73.
1993b. Relationship between size and depth in decapod populations on the slope between 900 and 2,200 m in the western Mediterranean. Deep-Sea Res. 4(11–12)2389–2400.

Sardà, F., and M. Demestre.
1987. Estudio biológico de la gamba *Aristeus antennatus* (Risso, 1816) en el Mar Catalán (NE de España). Inv. Pesq. 51 (1):213–232.
1989. Shortening of the rostrum and rostral variability in *Aristeus antennatus* (Risso, 1816) (Decapoda: Aristeidae). J. Crust. Biol. 9 (4):570–577.

Sardà, F., and P. Martin.
1986. Les pesqueries a Catalunya: evolució en els últims decennis. *In* J. Lleonart (ed.), L'Oceanografía, recursos pesquers de la mar Catalana. d'Ecol. Aplicada. Diputació de Barcelona 91–112.

Sardà, F., G. Y. Conan, and X. Fuste.
1993. Selectivity of Norway lobster (*Nephrops norvegicus*) in western Mediterranean. Sci. Mar. 57(2–3):167–174.

Sardà, F., C. Bas, and J. Lleonart.
In press. A functional morphometry of rose shrimp *Aristeus antennatus* (Risso, 1816) in western Mediterranean. Crustaceana.

Sousa, M. I.
1988. Sources of bias in growth and mortality estimation of migratory pelagic fish stocks, with emphasis on *Decapterus russelli* (Carangidae) in Mozambique. FAO Fish. Rep. 389:288–307.

Sparre, P., E. Ursin, and S. C. Venema.
1989. Introduction to tropical fish stock assessment. FAO Fish. Tech. Paper 306/1, 337 p.

Tobar, R., and F. Sardà.
1987. Análisis de la evolución de las capturas de gamba rosada, *Aristeus antennatus* (Risso, 1916), en los últimos decenios en Cataluña. Inf. Tec. del Inst. Ciencias del Mar de Barcelona (CSIC) 142:1–20.
1992. Annual and diel light cycle as a predictive factor in deep-water fisheries for the prawn *Aristeus antennatus* (Risso, 1816). Fish. Res. 15:169–179.

Tyler P. A.
1988. Seasonality in the deep sea. Oceanogr. Mar. Biol. Ann. Rev. 26:227–258.

Zar, J. H.
1984. Biostatistical Analysis. Prentice-Hall Inter., 718 p.

Abstract.— A 39-month study of the effects of cessation of sewage sludge disposal in the New York Bight apex on the diets of certain fishes and on the benthic macrofaunal community provided an opportunity to examine predator-prey relationships of winter flounder, *Pleuronectes americanus*, one of the common predators in the area. Benthic macrofauna and winter flounder were collected monthly and bimonthly, respectively, from July 1986 through September 1989 at three sites in the Bight apex that are variably influenced by sewage sludge. There were limited changes in winter flounder diets and abundance of dominant benthic macrofaunal species following cessation of sewage sludge disposal. The comparison of volumetric contribution of common prey in flounder stomachs to potential-prey abundance in benthic samples suggested several relationships. These included evidence of preferential predation on the polychaete *Pherusa affinis*; this selective preference may be associated with its high caloric content as well as with its average high biomass density. Other common prey, primarily polychaetes but including an anthozoan, were also preyed upon in proportions greater than their abundance in the environment. Some moderately abundant potential prey, such as the small near-surface-dwelling mollusc *Nucula proxima* and the ribbon worm *Cerebratulus lacteus* were not commonly preyed upon suggesting they were unavailable as prey or were avoided by winter flounder. Corresponding fluctuations in abundances and predation of the pollution-tolerant polychaete *Capitella* sp. and the pollution-sensitive amphipod *Unciola irrorata* suggested a proportional consumption relationship in association with sludge disposal and its cessation.

Predator-prey relationships of winter flounder, *Pleuronectes americanus*, in the New York Bight apex

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Predator diets provide information on sources of prey, predominant prey types, levels of particular prey use and availability, and prey preference or avoidance, when compared with the availability of potential prey in the environment (Levings, 1974; Diehl, 1992). For predatory fish such as winter flounder, *Pleuronectes americanus*, this information increases our understanding of prey selection, based on evidence of prey preference or avoidance, and how selective predation can affect or be affected by prey population dynamics.

In studies of aquatic environmental health, benthic macrofaunal diversity and certain indicator species are often used as response variables. Monitoring predator diets during such studies can aid in determining how predation can function as a confounding factor in interpreting macrofaunal change as solely the product of altered abiotic factors. Monitoring diets can also indicate how benthic species abundance and the overall community structure can be affected by predation. Predation studies can also aid in estimating the effect of benthic macrofaunal changes (natural or anthropogenic) on predator-prey relationships (i.e. loss of a seasonally or energetically important prey) or be used to define potential contaminant uptake pathways (Clements and Livingston, 1982; Gendron, 1987; Schindler, 1987).

Studies of the linkage between prey abundance and predation by marine fish are scarce, especially studies based on samples taken over an extended period of time or during an environmental change. An opportunity to examine predator-prey relationships was provided by the availability of the results of a comprehensive 39-month study of the effects of sewage sludge disposal abatement in the New York Bight apex (the coastal area at the mouth of New York Harbor). This study included monitoring the diets of several common fishes and large decapod crustaceans, the abundance of benthic macrofauna, as well as other biological and environmental variables (Environmental Processes Div., 1988).

The winter flounder, *Pleuronectes americanus* Walbaum (Robins et al., 1991) is an abundant demersal fish in the New York Bight apex. It was the third most important contributor (10%) to the total fish biomass collected during the study (Wilk et

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al., 1992). Winter flounder also rely almost entirely on small benthic macrofauna for food; thus, variability in predation and macrofaunal community structure can have important consequences for both the predator and its benthic prey (Kurtz, 1975; Clements and Livingston, 1982; Pihl et al., 1992).

This paper compares the diets of winter flounder with the abundance of benthic macrofauna at three stations in the New York Bight apex variably affected by sewage sludge, for evidence of 1) selective predation (preference or avoidance), 2) variation in the proportional consumption of benthic prey over time, and 3) the manner in which predator-prey relationships influenced the macrofauna with the cessation of sewage sludge disposal.

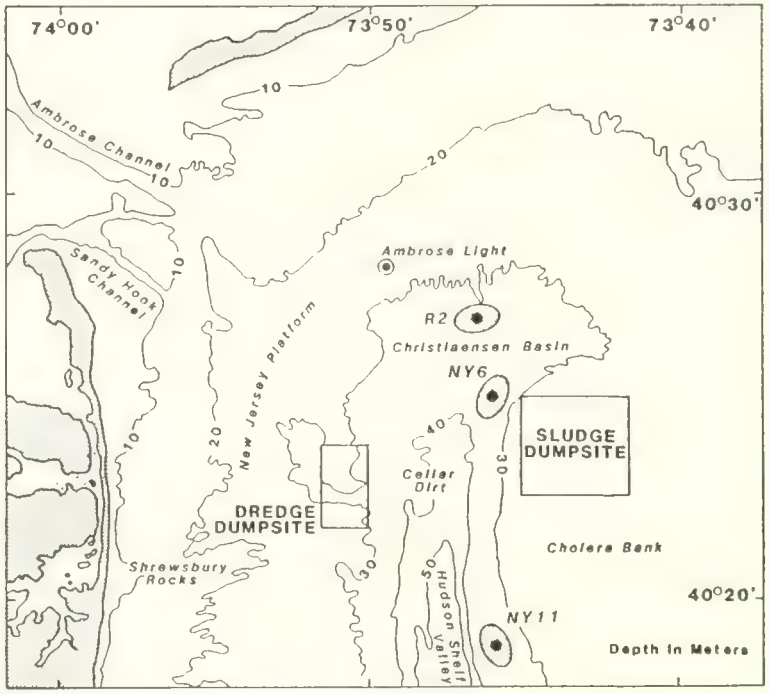


Figure 1

Location of stations and waste disposal sites in the New York Bight apex where winter flounder, *Pleuronectes americanus*, and benthic macrofauna were collected.

Materials and methods

Winter flounder and benthic macrofauna collection methods, sample processing, and primary data analyses for this study have been described in detail elsewhere (Reid et al. in press; Steimle, in press). In brief, three stations, R2, NY6, and NY11 (Fig. 1), were sampled systematically from July 1986 to September 1989 (Environmental Processes Div. 1988). These stations represent a gradient of conditions related to sewage sludge disposal, e.g. variable levels of total organic carbon (TOC) and chemical sediment contamination, such as chromium (Cr), that changed to some degree after cessation of disposal in December 1987 (Table 1). Station NY6 was the most sludge-affected area, with a markedly altered benthic community characterized by a relatively low species richness, low biomass, and high levels of TOC sediment contaminant such as Cr (Table 1). Station R2 was moderately affected by sludge and was biologically enhanced; it showed relatively high species richness and macrofaunal biomass and moderate levels of sediment contamination compared with NY6 (Table 1). Station NY11 was the least affected by sludge disposal, having relatively high species richness but low macrofaunal biomass and low levels of sediment contamination (Table 1). All stations were about 30 m in depth and had similar sediment types (silty-fine sands) and hydrographic characteristics (Table 1).

Triplicate benthic macrofaunal samples were collected monthly with a 0.1-m^2 Smith-McIntyre grab sampler and sieved through a 0.5-mm mesh screen. Materials retained were preserved in buffered formalin and later transferred to 70% ethanol. The samples were sorted and organisms were identified to the lowest possible taxon (usually species), counted, and moist-weighed (Reid et al., in press). Data from a total of 350 benthic macrofaunal samples were available for analysis.

Adult winter flounder were collected bimonthly (additional collections were made in August) with a small otter trawl at the same stations and during the same week as the benthic grab sampling. Each periodic trawl collection consisted of six daytime tows of 0.5 km, deployed in an array across the center of the station. Generally, at least 30 fish were collected from each station per collection period. Stomach contents were analyzed in the field or laboratory by using semi-quantitative, visual estimates of stomach volume from comparison of stomach boluses with variable-diameter, volume-calibrated cylinders. All identifiable items in the stomachs were identified to the lowest possible taxon and separated to visually estimate their individual percent contribution to total stomach volume (Langton et al., 1980; Steimle, in press). This method provides reasonable results compared with more labor intensive methods (Hyslop, 1980).

Table 1

Habitat characteristics (means) of three sampling sites in the New York Bight apex for the 18 months before (A) and 21 months after (B) sewage sludge disposal cessation; benthic biomass (wet wt) does not include the biomass of two large bivalves, *Pitar morrhuanus* and *Arctica islandica*.

	Stations					
	R2		NY6		NY11	
	A	B	A	B	A	B
Depth (m)	29		31		29	
Sediment						
grain size (phi)[1]	3.1	3.2	3.6	3.5	3.1	3.1
TOC (% dry wt)[1]	0.9	0.9	4.6	2.3	0.3	0.3
Cr (ppm dry wt)[2]	37.2	36.7	163.0	96.5	15.8	12.9
Bottom water[3]						
min. dissolved oxygen (mg/L)	4.2	5.7[4]	4.3	5.8[4]	5.3	5.5[4]
temp. range (°C)	~3–17 for all sites[5]					
Benthos						
biomass (g/m^2)	218.2	202.8	63.4	28.2	66.6	73.2
species (n)/grab	30	33	19	33	41	45

[1] Packer et al., in press.
[2] Zdanowicz et al., in press.
[3] Arlen, L., A. Draxler, and R. Bruno. Hydrographic observations in the bottom water of the New York Bight at the "12 mile" dumpsite: 1983–1990. Unpubl. manuscr.
[4] Dissolved oxygen content of <3 mg/L was recorded in September, 1989.
[5] Summer levels in 1988 were 2–3°C lower than the long-term mean.

The mean proportional volume (percent of the total volume) of a given prey item in the stomach was compared with the mean proportional biomass of that prey in the benthic macrofauna, and the relationship between these proportions was used to determine whether selective predation was evident. Although this approach to examining predator-prey associations differs from the traditional use of prey numerical abundance in stomachs and the environment, it is nonetheless realistic and useful because 1) prey volume can be a more precise dietary variable compared with uncertain enumeration of prey that are easily fragmented and for which only parts are present and 2) volume and biomass are approximately equivalent for most common prey taxa (see below). However, amphipods were also considered numerically because they are usually eaten whole and their exoskeletons are resistant to digestion and thus allow a reasonably accurate assessment of the number of individuals eaten.

The stomachs of 3,556 adult winter flounder, 18–30 cm total length, examined from the three study sites had identifiable food in them. To examine overall predator-prey relationships, stomach content and benthic data from the entire study period were pooled for each station because there were only minor changes in dominant prey and benthic species associated with sludge disposal cessation (Reid et al., in press; Steimle, in press). The use of pooled stomach content data to estimate prey preference by a predator population is recommended by some authors, e.g. Rachlin et al. (1987). Changes in predator-prey relationships related to cessation of sludge disposal are considered separately. Any seasonal or annual variability was assumed to be distributed equally within the pooled data as there were no gaps in collections. Log transformation of Shorigin's forage ratio index ($K=rt/pt$), adapted from a numerical approach for prey volume and biomass, was used to estimate prey selectivity (Berg, 1979): $K = \mathrm{Log}_{10}(rt/pt)$, where rt = proportion of prey in the diet estimated by contribution to stomach volume and pt = proportion of prey in the benthic biomass. Positive K values suggest a degree of selective predation. Near-zero K values suggested that predation is directly proportional to abundance. Negative K values suggest underutilization or avoidance of a potential prey relative to its availability.

The use of volume and biomass to calculate K is reasonable because 1 mL or cm^3 of prey volume is considered approximately equivalent to 1 g of macrofauna wet weight (Bowman, 1986). We partially verified this assumption by determining the mean volume to wet weight ratios for a number of individuals for a range of common prey taxa. The ratios for an

anthozoan, *Ceriantheopsis americanus*, a polychaete, *Pherusa affinis*, and the sand shrimp *Crangon septemspinosa* varied between 0.96 and 1.00 (n=≥26). However, the ratios for calcareous-shelled prey were lower, 0.70 for the bivalve mollusc *Nucula proxima* (n=50), and 0.77 for the sand dollar *Echinarachnius parma* (n=30).

All fish were collected near mid-day; therefore, the effects of digestion on stomach volume estimates were not considered a major factor. Winter flounder are primarily daytime feeders and all but the most soft-bodied prey should remain identifiable in their stomachs for several hours (MacDonald et al., 1982).

Results

Diet spectrum and dominance

Forty-nine prey taxa were identified in winter flounder stomachs, although only about 30 taxa were identified in the stomach contents at any individual station (Table 2). These are conservative estimates because of some uncertainties in identification caused by digestion. This prey spectrum represents about a quarter of the total available benthic macrofaunal taxa identified at station NY6 (119 species) and R2 (133 species), and about a fifth of the 154 species identified at station NY11.

Dominant prey, defined as species that composed at least 2% of the total stomach volume of fish from any station, were the polychaetes *Pherusa affinis*, *Asabellides oculata*, and *Nephtys incisa* and the tube-dwelling anthozoan *Ceriantheopsis americanus*. The rhynchocoel *Cerebratulus lacteus*, juvenile rock crabs *Cancer irroratus*, and other polychaetes, including *Capitella* sp. and *Scoletoma (Lumbrineris)* spp., were dominant in the diet at one or two stations (Table 3). Collectively these eight taxa constituted between 76% and 96% of the winter flounder diet by volume at the three stations (Table 3).

Predation patterns

The log forage ratio (K) indices were positive for several dominant species. The K index was consistently high (≥+0.25) for the polychaetes, *P. affinis* and *A. oculata*. High positive K values were also calculated for other prey, but at only one or two stations (Table 3). The K indices were near zero (±0.20) for some dominant species at some stations, such as *C. americanus*. For other prey or at other stations the K indices were low (<–0.25). This was especially evident for *C. americanus*, *Spio setosa*, *Glycera* sp., and the molluscs (Table 3).

Comparison of the contributions of these dominant prey species to flounder diets and to macrofaunal

Table 2

List of winter flounder, *Pleuronectes americanus*, prey identified in stomachs collected from three stations in the New York Bight apex.

	Station		
Prey	R2	NY6	NY11
Algae	X	X	
Coelenterates			
Ceriantheopsis americanus	X	X	X
Hydrozoans	X		X
Rhynchocoels	X	X	X
Nematodes		X	
Chaetognaths			X
Bryozoans		X	
Molluscs			
Nucula proxima	X	X	X
Yoldia sp.			X
Nudibranchia			X
Ilyanassa trivittata		X	
Polychaetes			
Nephtys sp.	X	X	X
Nephtys incisa	X	X	X
Ninoe nigripes	X		
Scoletoma (Lumbrineris) sp.	X	X	X
Scoletoma acicularum			X
Pherusa affinis	X	X	X
Asabellides oculata	X	X	X
Ampharete acutifrons		X	
Spionidae		X	X
Spio setosa	X		X
Spiophanes bombyx	X	X	X
Cirratulus cirratus		X	
Tharyx sp.	X		
Tharyx acutus	X	X	X
Capitella sp.	X	X	X
Mediomastus ambiseta	X		
Phyllodoce arenae	X		X
Drilonereis sp.	X	X	X
Glycera sp.	X	X	X
Ophioglycera gigantea	X		
Chone infundibuliformis			X
Aglaophamus circinata	X		
Nereis succinea		X	
Isopods			
Edotea triloba	X	X	X
Cirolana sp.		X	
Cumaceans			
Diastylis sp.	X	X	X
Amphipods			
Leptocheirus pinguis	X	X	X
Unciola irrorata	X	X	X
Monoculodes edwardsi		X	X
Photis pollex			X
Dyopedos sp.		X	
Mysids	X		
Decapods			
Cancer sp.	X	X	X
Cancer irroratus	X	X	X
Crangon septemspinosus	X	X	X
Echinoderms			
Echinarachnius parma			X
Tunicates			
Molgula sp.	X		
Salpidae		X	X

Table 3

Comparison of the average contribution of dominant prey in the diet of winter flounder, *Pleuronectes americanus* (mean % total stomach volume), to that of prey and dominant benthic infauna (infn) species (mean % total wet weight biomass) at stations in the New York Bight apex, 1986–1989. Seventy two benthic grab samples (triplicate samples at 24 collection periods) are included. K' is the log forage ratio.

	Stations								
	NY6			R2			NY11		
Species	prey	infn	(*K'*)	prey	infn	(*K'*)	prey	infn	(*K'*)
Ceriantheopsis americanus	28.0	18.5	0.18	7.0	6.6	0.03	27.3	6.4	0.63
Pherusa affinis	25.1	2.7	0.97	76.3	42.8	0.25	48.3	9.7	0.70
Asabellides oculata	9.2	3.8	0.38	3.4	<0.1	>1.83	2.0	<0.1	>1.60
Nephtys incisa	3.5	3.5	0	4.9	4.9	0	2.0	0.7	0.46
Capitella sp.	6.0	11.7	−0.29	0.3	<0.1	>0.78	<0.1	<0.1	0
Cerebratulus acteus	3.0	45.3	−1.15	2.4	2.0	0.08	0.8	2.0	−0.40
Scoletoma sp.	1.5	<0.1	>1.48	2.1	<0.1	>1.62	4.1	3.3	0.09
Cancer irroratus	11.3	2.4	0.67	1.5	4.4	−0.47	1.2	0.3	0.60
Spio setosa	<0.1	0.6	<−1.10	<0.1	0.1	<−0.30	0.8	7.5	−0.96
Nucula proxima	0.1	1.9	−1.30	<0.1	0.5	<−1.00	0.1	6.6	−1.70
Glycera sp.	0.6	0.8	−0.12	<0.1	0.2	<−0.60	0.1	6.5	−1.70
Pitar morrhuanus	0.0	0.1	−∞	0.0	30.7	−∞	0.0	14.7	−∞
Arctica islandica	0.0	0.1	−∞	0.0	<0.1	−∞	0.0	28.1	−∞
Ensis directus	0.0	<0.1	−∞	0.0	3.1	−∞	0.0	<0.1	−∞
Totals	78.2[1]	91.8		97.9	95.3		86.6	85.8	
Nonempty stomachs (*n*)	1405			1628			523		

[1] Diet residuals at this station were primarily (~11%) unidentifiable organic and inorganic material

biomass over time illustrates trends in the predator-prey association not evident in the pooled data (Table 3). For example, there was an apparent proportional consumption association (level of prey consumption was closely associated with level of abundance) for the anemone *C. americanus* at all stations, although the strength of the association varied at times (Fig. 2).

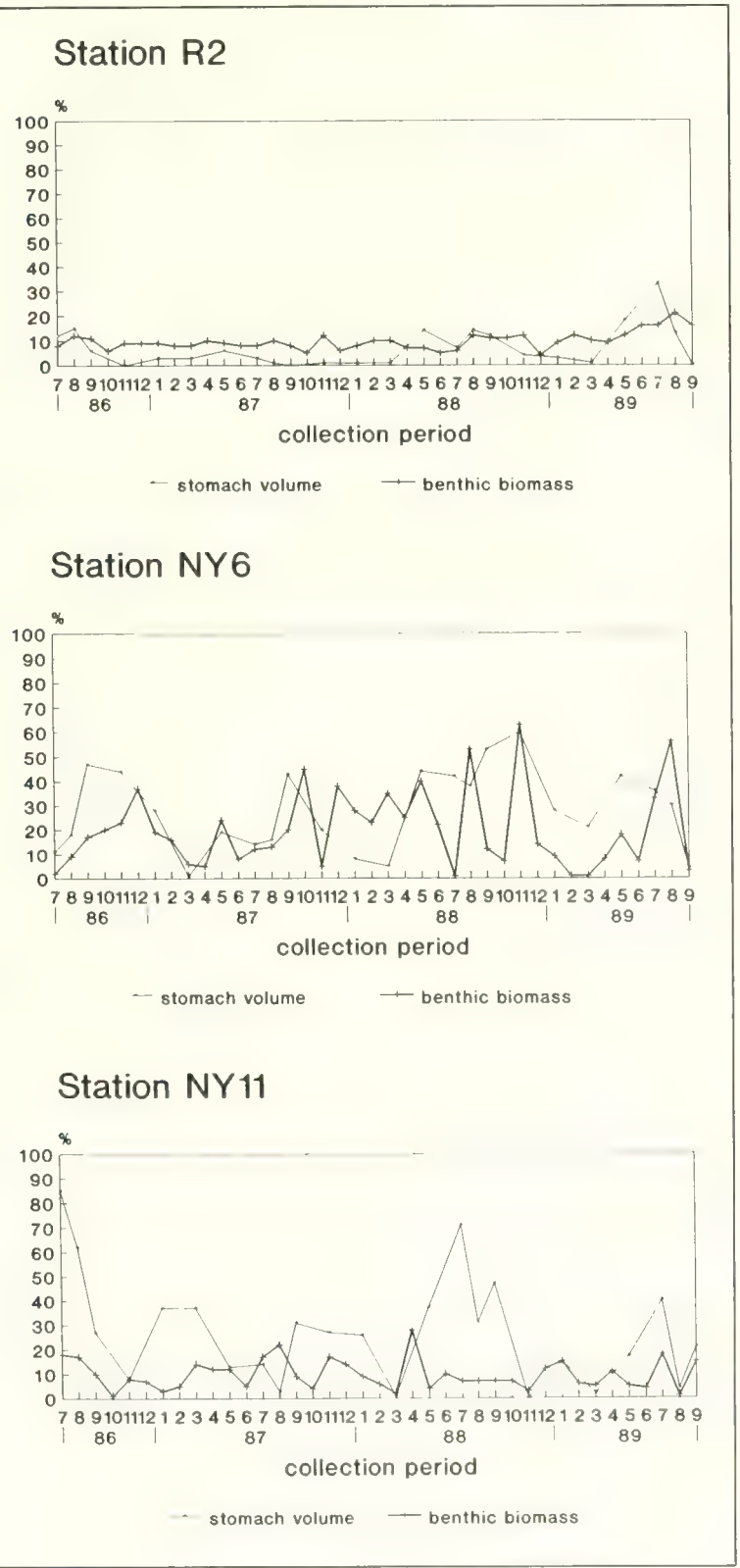
However, the proportional contribution of the polychaete *P. affinis* to winter flounder diets was greater than the prey's proportional contribution to total benthic macrofaunal biomass (Table 3, Fig. 3). The contribution of this prey to the winter flounder diet generally paralleled its contribution to macrofaunal biomass at all stations during the study period. Peaks in consumption are often consistent with peaks in proportional contribution to total community biomass, especially at stations NY6 and NY11 (Fig. 3). For the entire study period, the difference in proportional consumption and biomass for *P. affinis* ranged from 9.3 fold at station NY6 (25.1% stomach volume vs. 2.7% benthic biomass; K=0.97) to 1.8 fold at station R2 (76.3% volume vs. 42.8% biomass; K=0.25); station NY11 had an intermediate difference of 3.7 fold and K=0.70 (Table 3).

Some benthic species that were dominant in the overall benthic biomass were seldom identified in the flounder stomachs. For example, the rhynchocoel *C. lacteus*, which was particularly abundant at station NY6, was not often found in flounder stomachs, despite its relative importance in the benthic biomass (Table 3). This underutilization of potential prey was also evident at station NY11, where the polychaetes, *Glycera* spp. (mostly *G. dibranchiata*) and *Spio setosa*, as well as several mollusc species, composed >5% of the mean macrofauna biomass but were never important items in the flounder diet (Table 3). However, a substantial portion of the small, unidentified polychaete fragments found in some winter flounder stomachs may have been *S. setosa*. The predation-abundance trends over the study period for these and other less common prey are not presented but were similar to the trends presented for *C. americanus* (Fig 2).

In general, there was little evidence of predation on molluscs by winter flounder, despite their sometimes high contribution to overall macrofaunal biomass. For example, the minute (<5 mm shell width) Atlantic nut clam, *Nucula proxima*, a consistent, although only moderate component of the infaunal biomass, was not commonly found in winter flounder stomachs (Table 3).

Cessation of sewage sludge disposal

The change in abundance of two benthic species, the polychaete *Capitella* sp. and the amphipod *U. irrorata*, was associated with the cessation of sludge disposal (Reid et al., in press). These changes were also reflected in the occurrence of these two prey in winter flounder stomachs. When sludge disposal ended in 1987, the abundance of the stress-tolerant *Capitella* sp. declined and so did its occurrence in stomachs at station NY6 (Fig 4). For the more stress-sensitive *U. irrorata*, predation was also generally associated with abundance at two stations (Fig. 5). At station NY6, where the effect of sludge disposal was greatest, the abatement of sludge disposal was accompanied by a seasonally varying increase in the abundance of this amphipod and a corresponding increase in the frequency of occurrence in winter flounder stomachs (Fig. 5).



Discussion

Diet spectrum and dominance

The spectrum of prey and dominant prey taxa consumed by winter flounder in the New York Bight apex (Table 2) is similar to that reported in other winter flounder diet studies (Wells et al., 1973; Hacunda, 1981; Langton and Bowman, 1981; Bharadwaj, 1988; Steimle and Terranova, 1991). Winter flounder diet studies in estuaries and to the north also report the dominance of similar prey taxa (Tyler, 1972; Wells et al., 1973; Worobec, 1982). With the possible exception of *Capitella* sp., dominant prey are usually macroscopic, supporting Keats' (1990) hypothesis that winter flounder show a preference for the largest available prey that can be consumed.

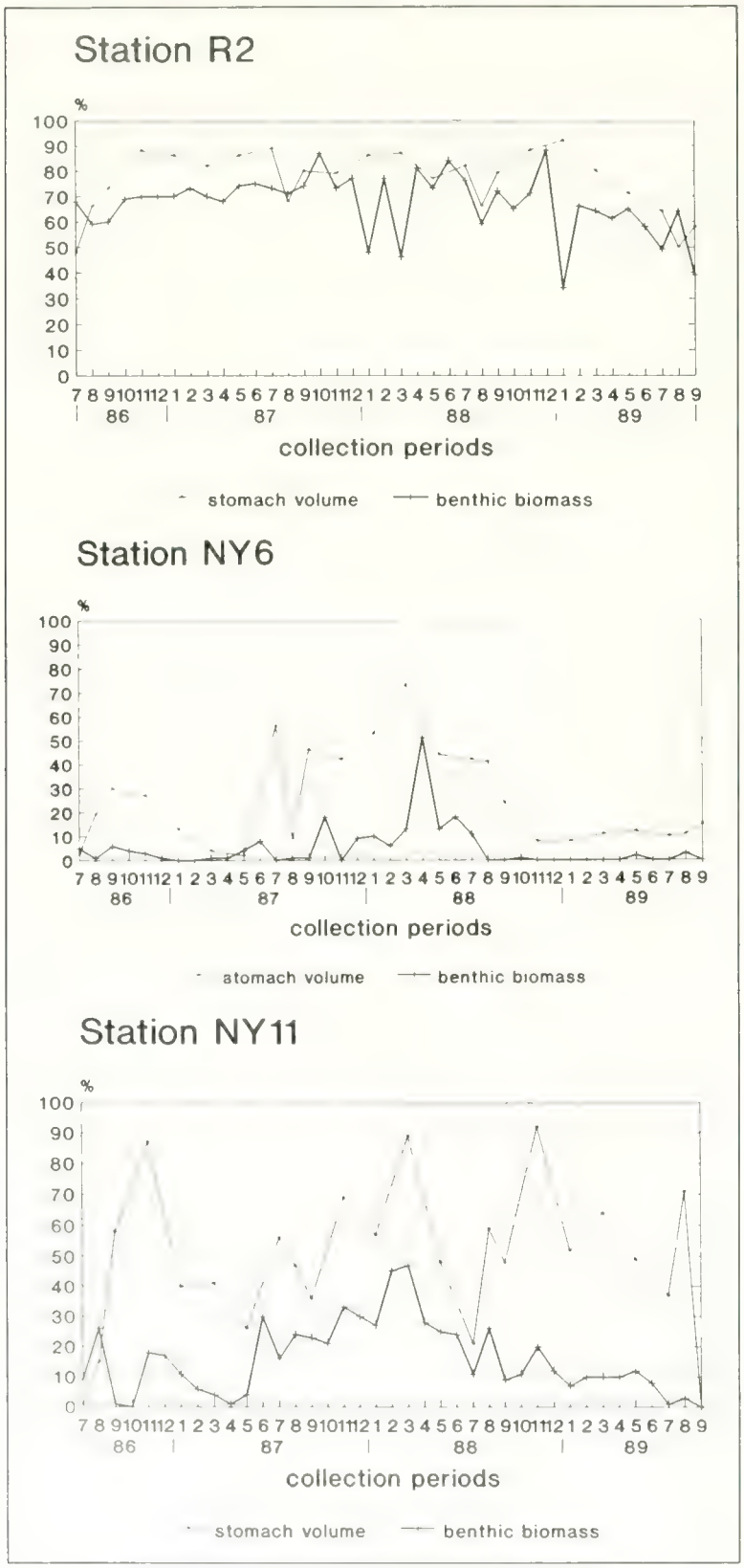
Predation patterns

The results of this study provide evidence that some prey species are consumed preferentially, but this was not temporally or spa-

Figure 2

Trends in the percent contribution of the burrowing anemone *Ceriantheopsis americanus* to total stomach volume of winter flounder, *Pleuronectes americanus*, compared to the anemone's percentage of the total benthic macrofaunal biomass at three sites in the New York Bight apex variably affected by sewage sludge disposal. Disposal gradually abated during 1987 and ceased by December 1987.

tially consistent. The parallel temporal relationship of the contribution of the anemone *C. americanus* to overall benthic biomass and to winter flounder diets at stations R2 and NY6 (Fig. 2) suggests a proportional consumption association. The forage ratio indices (K) for this prey are near zero (0.03 to 0.18, Table 3); these suggest that winter flounder neither preferred nor avoided this prey, consuming it at a level closely related to its availability at these two stations. Although, this relation was more variable at station NY11 (Fig. 2), a moderately high, positive K value (0.63) suggests some preference for this prey (Table 3).



The proportional consumption differences (Fig. 3) and strong positive K values at each station for *P. affinis* (Table 3) strongly suggest that winter flounder have a preference for this prey. Heavy predation on *P. affinis* may be energetically advantageous to winter flounder because this species has a high caloric equivalence ($\bar{x}$=1.9 Kcal/g wet weight; Steimle and Terranova, 1985). This is about double that of other major prey, which range from 0.9 to 1.1 Kcal/g wet weight, although some amphipod species, such as *U. irrorata* (consumed to a minor extent), are equally energy rich (Steimle and Terranova, 1985). The energy content of prey has been discussed as an important consideration in optimum foraging theories (Mangel and Clark, 1986) and the winter flounder preference for this high energy prey provides support for these theories. It is also possible that preference for this prey is related to the long-term dominance of *P. affinis* in the macrofauna of siltier areas of the New York Bight apex, as this relatively productive species has been common in the area and has been preyed upon since at least the mid-1960's (Steimle and Stone, 1973; Steimle, 1985, 1990; Steimle et al., 1990). This extended period of dominance may have contributed to winter flounder becoming experienced predators on this species (and other abundant prey species) and thus maintaining the preference (Gendron, 1987).

Figure 3

Trends in the percent contribution of the polychaete *Pherusa affinis* to total stomach volume of winter flounder, *Pleuronectes americanus*, compared to the polychaete's percentage contribution of the total benthic macrofaunal biomass at three sites in the New York Bight apex variably affected by sewage sludge disposal.

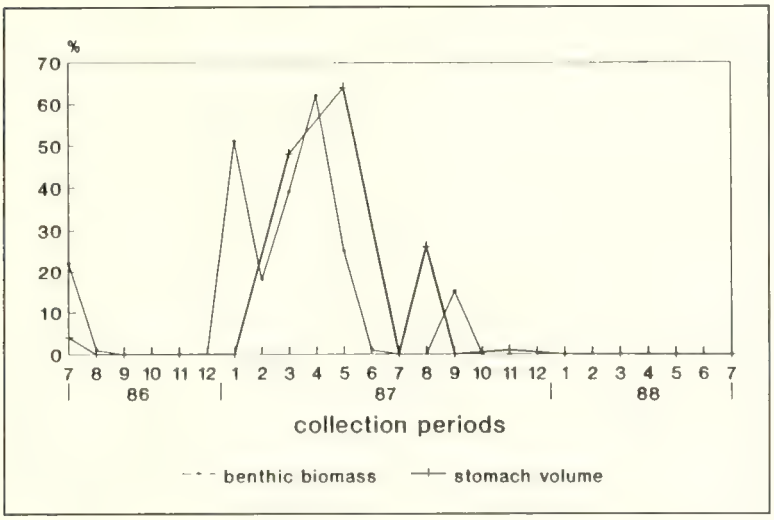
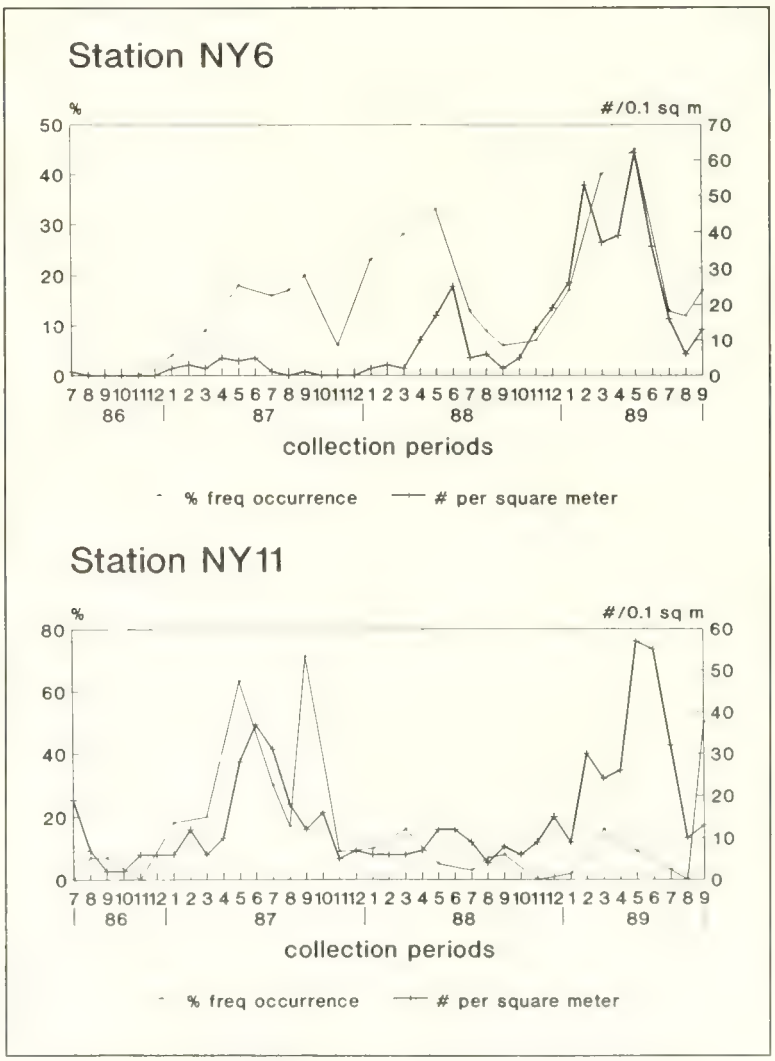


Figure 4

Trends in the percent contribution of the pollution-tolerant polychaete *Capitella* sp. to total stomach volume of winter flounder, *Pleuronectes americanus*, compared to the polychaete's percentage contribution to total benthic macrofaunal biomass at NY6, the station most affected by sewage sludge disposal and its cessation, in the New York Bight apex.

Figure 5

Trends in the frequency of occurrence of the amphipod *Unciola irrorata* in the diet of winter flounder, *Pleuronectes americanus*, compared to its numerical abundance in the benthic macrofaunal community at two stations in the New York Bight apex variably affected by sewage sludge disposal and its cessation in December 1987.



With the exception of *P. affinis* and perhaps *C. irroratus*, there is limited evidence of prey preference by winter flounder. This is consistent with the results of many qualitative winter flounder feeding studies that report a diverse diet, but also with limited evidence of a prey species' preferences (Tyler, 1972; Klein-MacPhee, 1978; Keats, 1990).

However, several dominant members of the benthic macrofaunal community at the three study stations were not commonly consumed by winter flounder. This underutilization may be related to prey size, burrowing depth, defense or escape mechanisms, or a variety of other factors (Main, 1985). For example, there was limited predation on *C. lacteus*, a major contributor to benthic biomass at station NY6. This nonproportional consumption or possible "avoidance" of this species is evident in the difference between the proportional consumption and abundance levels at this station (3.0% stomach volume vs. 45.3% benthic biomass) and the strong negative K (−1.15; Table 3); this difference at NY6 was fairly consistent over the study period (Fig. 6). Proportional predation or slight underutilization of this prey was evident at the other stations where it was less abundant and K ranged from +0.08 to −0.40 (Table 3).

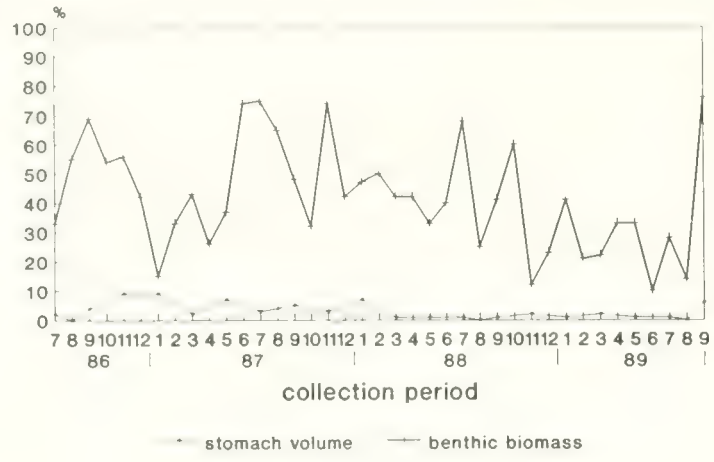


Figure 6

Trends in the percent contribution of the rhynchocoel *Cerebratulus lacteus* to the total stomach volume of winter flounder, *Pleuronectes americanus*, compared to the rhynchocoel's percentage contribution to total benthic macrofaunal biomass at NY6, the station most affected by sewage sludge disposal and its cessation, in the New York Bight apex.

The limited predation on *C. lacteus* could be related to its possession of defensive toxins in its tissues or to secretion of mucus that is strongly acidic, both of which can be offensive to potential predators (Kem, 1985; McDermott and Roe, 1985). Paradoxically, rhynchocoels are collected for fish bait in some areas and eaten by other fishes. It is possible, however, that this rhynchocoel's large size (>100 cm in length and >2 cm in width; Gosner, 1971), not its reported toxicity, is responsible for its limited use as prey for the small-mouthed winter flounder.

The underutilization of the small bivalve mollusc *N. proxima* (Table 3) is probably the result of its lack of availability as this species burrows into the sediment. The other molluscs common in the area, such as *P. morrhuanus*, *A. islandica*, *Ilyanassa trivittata*, and *Ensis directus*, are probably either too large or deeply buried to be suitable prey for winter flounder. However, *N. proxima*, as well as these other molluscs, except *P. morrhuanus*, were noted as prey in the diets of winter flounder elsewhere (Kurtz, 1975; Gilbert and Suchow, 1977; Klein-MacPhee, 1978; MacDonald et al., 1982; Worobec, 1982). The molluscan contribution to winter flounder diets in Narragansett Bay, Rhode Island, was also considered negligible (Bharadwaj, 1988).

Cessation of sewage sludge disposal

The cessation of sewage sludge disposal was expected to result in a substantial change in abundance of disposal-sensitive species in the benthic macrofaunal community. Any macrofaunal changes because of cessation were expected to be reflected in some predation variables (Spies, 1984; Cross et al., 1985; Environmental Processes Division, 1988). However, the only significant changes in the benthic community detected after cessation from 1987 to 1990 were in the overall abundance of a few pollution-tolerant or pollution-sensitive taxa, such as the polychaete *Capitella* sp. or amphipods at station NY6, nearest to the former disposal area. The abundance of other dominant benthic species at NY6, such as *P. affinis*, *N. incisa*, and *C. americanus*, did not change to any significant degree (Reid et al., in press).

The pollution-tolerant *Capitella* sp. has been a consistent, but variably abundant (hundreds to tens of thousands of individuals/m^2), member of the degraded benthic community at station NY6 since at least the early 1970's (Caracciola and Steimle, 1983). Its density in the macrofauna declined drastically (<100 individuals/m^2) after the cessation of sewage sludge disposal (Reid et al., 1991). Predation by winter flounder on this prey is probably related to the response of *Capitella* sp. to cessation of disposal.

There were increases in abundance of contaminant-sensitive amphipods, especially *Photis pollex* and *U. irrorata*, at station NY6 after disposal abatement began in 1987. Although contributions of amphipods to winter flounder diets were generally less than 1% of total stomach volumes (and thus not included in Table 3), numerical increases in amphipod abundance in the macrofaunal community coincided with increases in their frequency of occurrence in winter flounder stomachs. The general increase in the numerical abundance of one amphipod, *U. irrorata*, in benthic samples at NY6, especially after cessation, was accompanied by a corresponding increase in their occurrence in winter flounder stomachs (Fig. 5). However, a similar predation relationship for this prey was somewhat evident at station NY11, which was minimally affected by sludge disposal and cessation (Fig. 5). At both stations, the frequency of occurrence of *U. irrorata* in the diets closely paralleled seasonal (winter-spring) peaks in abundance, including reduced predation during an apparently poor recruitment year at NY11 in 1988 (Fig. 5). If the effects of the sludge were more general and included some effect at NY11, the pattern of predation on this species, which increased in abundance after cessation, could be associated with this cessation.

Predation influence on benthic populations and energetics

Strong selective predation by winter flounder on certain benthic macrofaunal taxa can influence the population dynamics of these prey and be a factor in interpreting benthic community change relative to disposal abatement. This affect may be evident in the predation-abundance patterns for *Capitella* sp., although the decline in the abundance of this species could be a result of its short life span as well as predation.

A short life span is not a factor for *P. affinis* as it lives for up to two years (Steimle et al. 1990). However, since winter flounder are visual predators (Klein-MacPhee, 1978; Bharadwaj, 1988), *P. affinis* may be at greater risk to predation because it is relatively large (up to 7.5 cm in length and 0.5 cm in width) and lives in vertical burrows with its fanned, setaceous cephalic cage (head and bristles) usually exposed. It also actively probes the sediment surface with feeding palps that may attract predator attention (J. Vitaliano, personal observ.; P. Ferri[1]). The persistent abundance and strong predation on *P. affinis* by winter flounder (Fig. 3) and other predators at station R2 (Steimle and Terranova, 1991; Steimle, in press) is interesting in that it suggests that this prey must be very productive in this area to sustain heavy predation pressure. This suggestion is supported by results of a previous study of the secondary production of this species that found it to be almost twice as productive near R2 as at NY6 and NY11 (Steimle et al., 1990).

The results of this study are subject to potential biases inherent in most stomach content analyses, such as differential digestion of different prey types (MacDonald et al., 1982). Partial digestion of prey can underestimate a prey's contribution to diets based on stomach volume. Thus, the estimated proportional contribution to diets of some soft-bodied prey will be conservative. This study also assumes that the stomach contents of fish represented feeding at or very near where the benthic infauna samples were collected (Steimle, in press) and that if a large proportion of the prey was consumed in nearby areas, the benthic community structure did not differ substantially from that at the actual benthic collection site. Some preliminary data from peripheral benthic stations sampled during the study suggest that this assumption was valid, although there were substantial changes in community structure in some parts of the trawling zones (Fromm, personal observ.).

In summary, diets of winter flounder in the New York Bight apex 1) were dominated by a few prey species, typically polychaetes, an anthozoan, and small crustaceans; 2) showed a preference for the energy-rich polychaete *Pherusa affinis*; 3) suggested there was underutilization or "avoidance" of molluscs and rhynchocoels; and 4) showed that apparent responses of some benthic macrofaunal species (*Capitella* sp. and *U. irrorata*) to cessation of sludge disposal and natural fluctuations in abundance were reflected in corresponding changes in their use as prey.

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Literature cited

Berg, J.
1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). Mar. Biol. 50:263–273.

Bharadwaj, A.
1988. The feeding ecology of the winter flounder, *Pseudopleuronectes americanus* (Walbaum), in Narragansett Bay, Rhode Island. M.S. thesis, Univ. Rhode Island, Kingston, RI, 129 p.

Bowman, R. E.
1986. Effects of regurgitation on stomach content data of marine fishes. Environ. Biol. Fish. 16:171–181.

Caracciola, J. V., and F. W. Steimle.
1983. An atlas of the distribution and abundance of dominant benthic invertebrates in the New York Bight apex with reviews of their life histories. NOAA Tech. Rep. NMFS SSRF-766, 58 p.

Clements, W. H., and R. J. Livingston.
1982. Overlap and pollution-induced variability in the feeding habits of filefish (Pisces: Monacanthidae) from Apalachee Bay, Florida. Copeia 2:331–338.

Cross, J. N., J. Roney, and G. S. Kleppel.
1985. Fish food habits along a pollution gradient. Calif. Fish Game 71:28–39.

Diehl, S.
1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73:1646–1661.

Environmental Processes Division.
1988. Plan for study-response of habitat and biota of the inner New York Bight to abatement of sewage sludge dumping. NOAA Tech. Memo. NMFS F/NEC-55, 34 p.

[1] Ferri, P., U.S. Environmental Protection Agency, Narragansett, RI 02882. Personal Commun., 1992.

Gendron, R. P.
1987. Models and mechanisms of frequency-dependent predation. Am. Nat. 130:603–623.

Gilbert, W. H., and E. F. Suchow.
1977. Predation by winter flounder (*Pseudopleuronectes americanus*) on the siphons of the clam, *Tellina agilis*. Nautilus 91:16–17.

Gosner, K. L.
1971. Guide to identification of marine and estuarine invertebrates, Cape Hatteras to the Bay of Fundy. Wiley-Interscience, NY, 693 p.

Hacunda, J. S.
1981. Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. Fish. Bull. 79:775–788.

Hyslop, E. J.
1980. Stomach contents analysis—a review of methods and their application. J. Fish. Biol. 17:411–423.

Keats, D. W.
1990. Food of winter flounder *Pseudopleuronectes americanus* in a sea urchin dominated community in eastern Newfoundland. Mar. Ecol. Prog. Ser. 60:13–22.

Kem, W. R.
1985. Structure and action of nemertean toxins. Am. Zool. 25:99–111.

Klein-MacPhee, G.
1978. Synopsis of biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). NOAA Tech. Rep. NMFS Circ. 414, 43 p.

Kurtz, R. J.
1975. Stomach content analysis in relation to differences in growth rate of winter flounder (*Pseudopleuronectes americanus*) from two Long Island Bays. M.S. thesis, Long Island Univ., Greenvale, NY, 60 p.

Langton, R. W., and R. E. Bowman.
1981. Food of eight northwest Atlantic pleuronectiform fishes. NOAA Tech. Rep. SSRF-749, 16 p.

Langton, R. W., B. M. North, B. P. Hayden, and R. E. Bowman.
1980. Fish food habits studies—sampling procedures and data processing methods utilized by the Northeast Fisheries Center, Woods Hole Laboratory, USA. Int. Counc. Explor. Sea, C. M. 1980/L:61, 16 p.

Levings, C. D.
1974. Seasonal changes in feeding and particle selection by winter flounder (*Pseudopleuronectes americanus*). Trans. Am. Fish. Soc. 103:828–832.

MacDonald, J. S., K. G. Waiwood, and R. H. Green.
1982. Rates of digestion of different prey in Atlantic cod (*Gadus morhua*), ocean pout (*Macrozoarces americanus*), winter flounder (*Pseudopleuronectes americanus*) and American plaice (*Hippoglossoides platessoides*). Can. J. Fish. Aquat. Sci. 39:651–659.

Main, K. L.
1985. The influence of prey identity and size on selection of prey by two marine fishes. J. Exp. Mar. Biol. Ecol. 88:145–152.

Mangel, M., and C. W. Clark.
1986. Towards a unified foraging theory. Ecology 67:1127–1138.

McDermott, J. J., and P. Roe.
1985. Food, feeding behavior and feeding ecology of nemerteans. Am. Zool. 25:113–125.

Packer, D., T. Finneran, L. Arlen, R. Koch, S. Fromm, J. Finn, S. A. Fromm, and A. Draxler.
In. Press. Fundamental and mass properties of surficial sediments in the inner New York Bight and responses to the abatement of sewage sludge dumping. *In* A. Studholme, J. E. O'Reilly, and M. C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Pihl, L., S. P. Baden, R. J. Diaz, and L. C. Schaffner.
1992. Hypoxia-induced structural changes in the diets of bottom-feeding fish and Crustacea. Mar. Biol. 112:349–361.

Rachlin, J. W., A. Pappantoniou, and B. E. Warkentine.
1987. A bias estimator of the environmental resource base in diet preference studies with fish. J. Freshwater Ecol. 4:23–31.

Reid, R., D. Radosh, A. Frame, and S. Fromm.
1991. Benthic macrofauna of the New York Bight, 1979–89. NOAA Tech. Rep. NMFS 103, 50 p.

Reid, R., S. Fromm, A. Frame, D. Jeffress, J. Vitaliano, D. Radosh, and J. Finn.
In press. Limited responses of benthic macrofauna and selected sewage sludge components to phase-out of sludge dumping in the inner New York Bight. *In* A. Studholme, J.E. O'Reilly, and M.C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott.
1991. Common and scientific names of fishes from the United States and Canada (5th ed.). Am. Fish. Soc. Spec. Publ. 20.

Schindler, D. W.
1987. Detecting ecosystem responses to anthropogenic stress. Can. J. Fish. Aquat. Sci. 44 (Suppl.1): 6–25.

Spies, R.
1984. Benthic-pelagic coupling in sewage-affected marine ecosystems. Mar. Environ. Res. 13:195–230.

Steimle, F.
1985. Biomass and estimated productivity of the benthic macrofauna in the New York Bight: a stressed coastal area. Estuarine Coastal Shelf Sci. 21:539–554.
1990. Benthic macrofauna and habitat monitoring on the continental shelf of the northeastern United

States. I: Biomass. NOAA Tech. Rep. NMFS 86, 28 p.

Steimle, F. W.
In press. Effects of sewage sludge disposal abatement on winter flounder, red hake, and lobster feeding and diets in the New York Bight Apex. *In* A. Studholme, J. E. O'Reilly, and M. C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Steimle, F. W., and R. B. Stone.
1973. Abundance and distribution of inshore benthic fauna off southwestern Long Island, N.Y. NOAA Tech. Rep. NMFS SSRF-673, 50 p.

Steimle, F. W., and R. Terranova.
1985. Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. J. Northwest Atl. Fish. Sci. 6:117–124.
1991. Trophodynamics of select demersal fishes in the New York Bight. NOAA Tech. Memo. F/NEC-84, 11 p.

Steimle, F. W., P. Kinner, S. Howe, and W. Leathem.
1990. Polychaete population dynamics and production in the New York Bight associated with variable levels of sediment contamination. Ophelia 31:105–123.

Tyler, A. V.
1972. Food resource division among northern, marine, demersal fishes. J. Fish. Res. Board Can. 29:997–1003.

Wells, B. D., D. H. Steele, and A. V. Tyler.
1973. Intertidal feeding of winter flounder (*Pseudopleuronectes americanus*) in the Bay of Fundy. J. Fish. Res. Board Can. 30:1374–1378.

Wilk, S., R. Pikanowski, A. Pacheco, D. MacMillan, and L. Stehlik.
1992. Response of fish and megainvertebrates of the New York Bight apex to the abatement of sewage sludge dumping. NOAA Tech. Memo. NMFS F/NEC-90, 78 p.

Worobec, M. N.
1982. Field analysis of winter flounder *Pseudopleuronectes americanus* in a coastal pond: abundance, daily ration, and annual consumption. Ph.D. thesis, Univ. Rhode Island, Kingston, RI, 115 p.

Zdanowicz, V. S., S. L. Cunneff, and T. W. Finneran.
In press. Reductions in sediment metal contamination in the New York Bight apex with the cessation of sewage sludge dumping. *In* A. Studholme, J. E. O'Reilly, and M. C. Ingham (eds.), Effects of the cessation of sewage sludge dumping at the 12-mile site. NOAA Technical Rep. NMFS.

Rockfish assemblages of the middle shelf and upper slope off Oregon and Washington

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Abstract.—Numerical classification techniques, recurrent group analysis, and a clustering analysis that uses the Bray-Curtis resemblance measure were used to identify rockfish (family Scorpaenidae) assemblages in the offshore waters of Oregon and Washington. Catch data from six multispecies groundfish assessment surveys conducted at three-year intervals (1977–92) by the National Marine Fisheries Service's Alaska Fisheries Science Center revealed three assemblages. The first, a deep-water assemblage, consisted of shortspine thornyhead, *Sebastolobus alascanus*, Pacific ocean perch, *Sebastes alutus*, darkblotched rockfish, *S. crameri*, and splitnose rockfish, *S. diploproa*. Redbanded rockfish, *S. babcocki*, and rougheye rockfish, *S. aleutianus*, were closely associated with this group. The second assemblage consisted of canary rockfish, *S. pinniger*, yellowtail rockfish, *S. flavidus*, and greenstriped rockfish, *S. elongatus*. This group was most abundant in areas over the middle shelf. The third assemblage, closely associated with the second, consisted of sharpchin, *S. zacentrus*, rosethorn, *S. helvomaculatus*, and redstripe, *S. proriger*, rockfish. While the three assemblages may be of particular interest to ecologists, managers faced with the division of the *Sebastes* complex management unit into groups that better reflect rockfish cooccurrence may only be able to manage the latter two assemblages as one shelf-rockfish unit.

Over the last three decades, some stocks of the more than 30 species of rockfish (family Scorpaenidae) known to inhabit the offshore waters of Oregon and Washington (Eschmeyer and Herald, 1983) have been the target of intense foreign and domestic fishing pressure in a largely multispecies trawl fishery. In 1982 a groundfish fishery management plan was implemented by the Pacific Fisheries Management Council to address the reductions in groundfish populations, including serious declines of several rockfish species in some areas. This plan was based on an underlying single-species management philosophy.

In both the Columbia and the U.S. portion of the Vancouver (US-Vancouver) management areas instituted by the International North Pacific Fisheries Commission (INPFC), annual harvesting restrictions have been fashioned for Pacific ocean perch, *Sebastes alutus*, widow rockfish, *S. entomelas*, shortbelly rockfish, *S. jordani*, and thornyheads, *Sebastolobus* spp. The remaining rockfish species have been lumped into a single management unit, the *Sebastes* complex. In addition to individual trip limits, current restrictions for this large group involve an overall annual harvest guideline and harvest guidelines for two of its already stressed components, yellowtail, *Sebastes flavidus*, and canary, *S. pinniger*, rockfish (PFMC, 1992[1]). While efforts to prevent over-harvesting of yellowtail and canary rockfish continue, the fishing pressure on the minor rockfish in the management unit has escalated. Species, such as darkblotched rockfish, *S. crameri*, are becoming increasingly important to fishermen.

This research stems from a concern over the long-term effects of the trawl fishery on the condition of the rockfish community as a whole. Current reductions in some stocks along with present bycatch practices may precipitate the need for changes in management policies to conserve these stocks. One possible course of action involves multispecies management, whereby cooccurring species are managed as a species complex or assemblage. If needed, restrictions could be placed on the fishery for the assemblage when specific components become stressed. An effective assemblage management program requires knowledge of interspecific associations in addition to individual life histories, distribution, and abundance patterns.

Prior knowledge of offshore rockfish associations has largely been inferred from shoreside sampling of commercial catches. In recent years several investigations have been

[1] Pacific Fishery Management Council (PFMC). 1992. Status of the Pacific coast groundfish fishery through 1992 and recommended acceptable biological catches for 1993; stock assessment and fishery evaluation. Pacific Fishery Management Council, Metro Center, Suite 420, 2000 SW First Ave., Portland, OR 97201, 80 p.

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Fishery Bulletin 92:620–632 (1994)

conducted to identify assemblages using trawl data covering extensive geographic areas. Nagtegaal (1983) studied both annual and seasonal interrelationships of some rockfish species off British Columbia based on commercial catch data. However, these catch statistics do not allow a full description of the effects of selective harvest on the entire rockfish community, as the landed species are those of highest economic value allowed for harvest at the time and reflect only a portion of the overall rockfish community exposed to trawling. Rogers and Pikitch (1992) defined several groundfish assemblages based on prediscard data from the commercial trawl fishery off Oregon and Washington. That study included a variety of groundfish families, but only the most abundant rockfish species were considered. Similarly, Gabriel (1982) included a wide variety of groundfishes in a 1-year assemblage study that utilized 1977 survey data from California to Washington. All of these researchers recognized the value of fish assemblage identification as a tool for fisheries management and emphasized the need to verify assemblage persistence.

Since 1977, the Alaska Fisheries Science Center (AFSC) of the National Marine Fisheries Service (NMFS) has been conducting controlled bottom trawl surveys aimed at assessing and monitoring groundfish resources off the west coast of the United States. Now that several of these surveys have been performed, a unique opportunity exists to monitor persistence in fish assemblages. In this paper I describe and summarize these surveys and their rockfish samples and use standard numerical classification techniques to identify the major rockfish assemblages.

Methods

This study utilizes rockfish catch data from six AFSC multispecies groundfish assessment surveys conducted triennially over a 16-year period from 1977 to 1992. Only data from bottom trawling in the Columbia and U.S.-Vancouver INPFC areas (43°00'N to the U.S.-Canada border) were examined. Trawling occurred during August and September between the depths of 55 and 366 m. All surveys employed stratified random sampling designs, apportioning towing sites according to various geographic strata and depth intervals. While the overall multispecies assessment goal remained unchanged from one survey to the next, many of the specific objectives did not. Objectives of the 1977 survey included determining the distribution and abundance of several commercially important rockfishes (Gunderson and Sample, 1980) and the on-bottom component of Pacific hake, *Merluccius productus*. The survey design was patterned after rockfish distributions, determined by fisheries catch data and the results of a pilot rockfish survey (Gunderson and Nelson[2]). The 1980 survey was specifically redesigned to better assess the canary and yellowtail rockfish populations, in addition to Pacific hake (Coleman, 1986). Thus, the sampling effort was divided among three depth strata: 55–183 m, 184–220 m, and 221–366 m. The 1983 survey repeated the work conducted in 1980 with the addition of some stations in the northern U.S.-Vancouver area (Weinberg et al., 1984). Based on the results of the previous surveys and in an attempt to further reduce the variance of canary and yellowtail rockfish catch rates, station allocation was changed again in 1986 (Coleman, 1988). In that year, sampling was apportioned among four depth strata: 55–91 m, 92–183 m, 184–219 m, and 220–366 m. Almost three times the effort was applied in the U.S.-Vancouver area, most of which was off northern Washington (lat. 48°00'–42°23'N). However, having not been able to improve rockfish estimates significantly, the 1989 and 1992 AFSC surveys shifted away from rockfish concerns of past surveys and concentrated on abundance estimation of Pacific hake and young sablefish, *Anoplopoma fimbria*. Consequently, the high density rockfish strata were abandoned and sampling was allocated within only two depth strata, 55–183 m and 184–366 m (Weinberg et al., 1994).

Samples were collected with standardized Nor'eastern high-opening rockfish bottom trawls rigged with roller gear. In general the gear's horizontal and vertical openings measured 13 and 9 m, respectively. Towing was controlled by fishing along depth contours for one-half hour at about three knots. Catches were sorted by species, weighed, and counted.

Assemblage analyses

I examined rockfish associations using two techniques: recurrent group analysis and cluster analysis. These two methods provide somewhat different characterizations of species distribution and cooccurrence and, when used together, can enhance our understanding of rockfish communities.

Recurrent group analysis (RGA), a nonhierarchical technique, addresses the question of which rockfish are likely to be caught together, thus reflecting their

[2] Gunderson, D. R., and M. O. Nelson. 1977. Preliminary report on an experimental rockfish survey conducted off Monterey, California, and in Queen Charlotte Sound, British Columbia, during August-September 1976. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Northwest and Alaska Fish. Cent., 2725 Montlake Blvd. E., Seattle, WA 98112. Unpubl. manuscr., 82 p.

spatial distribution patterns (Fager and McGowan, 1963). Species were included in a group based solely on their presence or absence in catches. Fixed groups were defined as the greatest number of members having affinities with one another based on a 40% affinity threshold.

However, because fishermen are concerned primarily with abundance in terms of biomass, the findings of RGA were supplemented by cluster analysis (CA), a method that incorporates sample catch weights into the grouping process. CA calculates resemblance measures using the Bray-Curtis dissimilarity coefficient (Bray and Curtis, 1957) and then clusters agglomeratively, using a flexible sort fusion strategy with an assigned clustering coefficient value (beta) equal to –0.25 (Lance and Williams, 1967). The flexible strategy was selected over other clustering methods because of its tendency to reduce the chaining effect often seen in dendrograms. Dendrograms display the similarities among species and groups in hierarchical form, permitting greater flexibility in the interpretation of associations than the RGA technique which produces set groups (Clifford and Stephenson, 1975). Relative groupings can be distinguished at varying levels of dissimilarity where the number 0 indicates greatest resemblance.

Prior to classifying assemblages, steps were taken to reduce "noise" in the data. First, groundfish species other than scorpaenids were eliminated, since the objective of the study was to identify rockfish assemblages without the masking effect caused by the presence of other species. Next, the least frequent rockfishes, defined as those taken at fewer than three stations in each of the groundfish surveys, were omitted. Knowledge of the path width of our survey gear facilitated the standardization of catch data as catch per unit of effort (CPUE), i.e. kilograms per hectare towed (kg/ha)[3], or roughly equivalent to towing our gear for 0.8 km. Finally, CPUE's were log transformed ($\log_{10}(x+1)$) to reduce the influence of high CPUE's (Boesch[4]).

Results

Over the six surveys, a total of 1,874 successful hauls were made in the Columbia and U.S.-Vancouver INPFC areas (Fig. 1). Rockfish were present in 79% (1,476) of the tows. Sampling effort was greatest in 1986 and considerably lower during 1977, 1989, and 1992. Most of the effort was applied between the depths of 101 and 200 m (Fig. 2). Sampling at greater depths was proportionally higher in 1977 than during the other surveys.

Catch composition and species diversity

Thirty three rockfish species (shortspine thornyhead *Sebastolobus alascanus* and 32 species of *Sebastes*) were identified. Among these, 20 were commonly caught in 1,468 hauls and included in the assemblage analysis (Table 1).

Catches of rockfish varied widely in size and composition. Many of the catches were small: 25% had CPUE's under 1.1 kg/ha and 50% had CPUE's under 4.8 kg/ha. In contrast, 8% were greater than 100 kg/ha while only 1% were greater than 500 kg/ha. Maximum rockfish CPUE's reached 4,126, 564, 1,253, 759, 2,303, and 828 kg/ha during the six respective surveys. The average CPUE for each survey was 50, 16, 34, 21, 34, and 27 kg/ha, respectively. On average, abundance levels increased in deeper water, peaking in the 151–250 m depth interval (Fig. 3).

Species diversity in survey catches depicts the multispecies nature of the rockfish community vulnerable to the bottom trawl. Eighty three percent of rockfish samples contained more than one species. Of these, approximately 50% contained 2–5 species, 29% contained 6–10 species, and 4% contained 10–16 species. Of the single-species catches, 78% were under 1 kg/ha. In contrast, the two largest single-species catches (canary rockfish) exceeded 100 kg/ha. Eighty five percent of the single-species samples were either shortspine thornyhead (7%), canary (26%), darkblotched (21%), yellowtail (18%), or green-striped, *Sebastes elongatus* (14%), rockfish. Silvergray, *S. brevispinis*, rosethorn, *S. helvomaculatus*, redbanded, *S. babcocki*, and yellowmouth, *S. reedi*, rockfish were never caught alone.

Species diversity, like abundance, increased with depth (Fig. 4). Hauls made at the shallowest sampling sites (~55 m) demonstrated little variety. As sampling depth increased, nearshore species, such as black, *S. melanops*, and quillback, *S. maliger*, rockfish, were replaced by offshore rockfishes, including juveniles of many species that inhabit even deeper waters as adults. Over the middle-shelf, within the 55–150 m depth interval, up to 13 rockfish species were taken in a single tow. About 22% of the hauls made at these depths contained five or more species (Table 2). Species diversity peaked along the outer-shelf, where the centers of abundance for several species overlapped. In waters 151–250 m deep, catches

[3] 1 kg/ha=0.1 t/km^2.

[4] Boesch, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. Virginia Inst. Marine Science, Spec. Sci. Rep. 77, EPA-600/3-77-033, 114 p. Environ. Res. Lab., Off. Res. Dev., U.S. Environ. Protection Agency, Corvallis, OR 97330

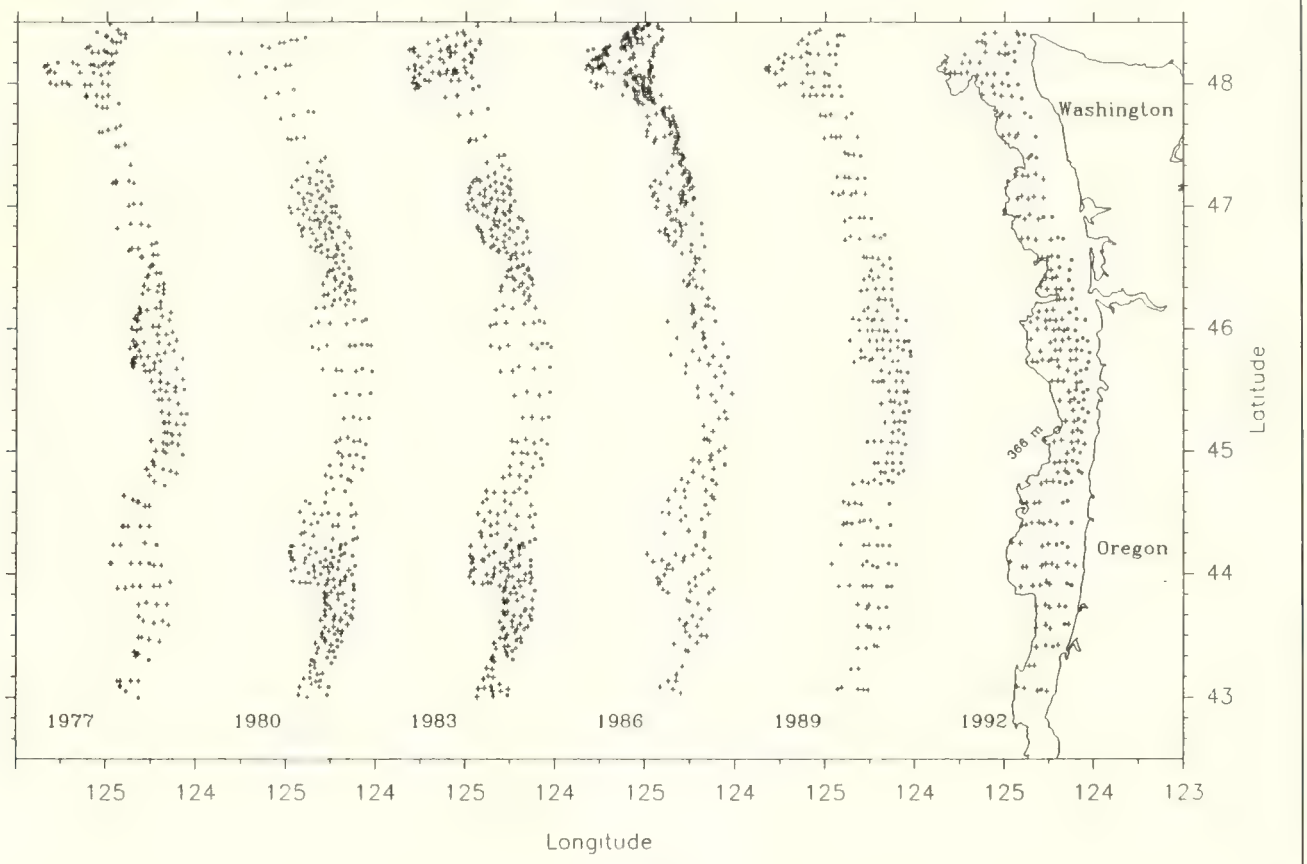

Figure 1

The distribution of hauls from the west coast triennial groundfish surveys showing the presence (+) or absence (o) of rockfish (Scorpaenidae) in the Columbia and U.S.-Vancouver areas.

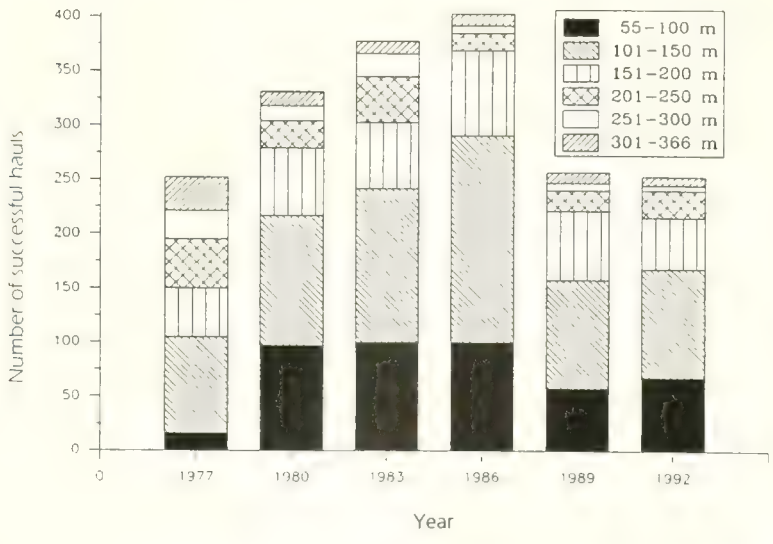

Figure 2

Distribution of successful survey effort by depth interval for the west coast triennial groundfish surveys (1977–92).

Table 1

The frequency of occurrence of rockfishes (Scorpaenidae) in the Columbia and U.S.-Vancouver areas from the west coast triennial groundfish surveys (1977–92).

Scientific name	Common name	Frequency of occurrence						
		1977	1980	1983	1986	1989	1992	Total
Species included in assemblage analyses								
Sebastolobus alascanus	Shortspine thornyhead	140	92	130	113	81	57	613
Sebastes aleutianus	Rougheye rockfish	39	19	36	54	47	46	241
Sebastes alutus	Pacific ocean perch	129	52	92	80	43	54	450
Sebastes babcocki	Redbanded rockfish	72	40	61	40	41	33	287
Sebastes brevispinis	Silvergray rockfish	31	23	54	34	11	8	161
Sebastes crameri	Darkblotched rockfish	129	99	172	163	128	105	796
Sebastes diploproa	Splitnose rockfish	90	38	90	56	50	33	357
Sebastes elongatus	Greenstriped rockfish	98	92	191	185	123	124	813
Sebastes entomelas	Widow rockfish	45	23	45	36	17	24	190
Sebastes flavidus	Yellowtail rockfish	90	83	153	130	44	53	553
Sebastes helvomaculatus	Rosethorn rockfish	42	36	64	59	46	48	295
Sebastes jordani	Shortbelly rockfish	5	46	39	28	11	5	134
Sebastes paucispinis	Bocaccio	45	36	60	34	10	3	188
Sebastes pinniger	Canary rockfish	74	68	143	155	63	50	553
Sebastes proriger	Redstripe rockfish	29	27	47	43	37	28	211
Sebastes reedi	Yellowmouth rockfish	6	4	11	6	4	8	39
Sebastes ruberrimus	Yelloweye rockfish	13	12	23	26	24	19	117
Sebastes saxicola	Stripetail rockfish	35	26	45	27	26	24	183
Sebastes wilsoni	Pygmy rockfish	3	7	21	20	27	13	91
Sebastes zacentrus	Sharpchin rockfish	74	39	82	77	53	48	373
Species excluded from assemblage analyses								
Sebastes aurora	Aurora rockfish	1		2			1	4
Sebastes borealis	Shortraker rockfish	5	1	3	2	—		11
Sebastes chlorostictus	Greenspotted rockfish	1	5	1	2	1	3	13
Sebastes eos	Pink rockfish	2	—	—			—	2
Sebastes goodei	Chilipepper	—	4	4	1	3	1	13
Sebastes levis	Cowcod		—	—	—	2	1	3
Sebastes maliger	Quillback rockfish	1	—	1	5	2	3	12
Sebastes melanops	Black rockfish		4	7	10	2		23
Sebastes melanostomus	Blackgill rockfish		4	1	—	—	—	5
Sebastes nigrocinctus	Tiger rockfish	—		1		—		1
Sebastes ovalis	Speckled rockfish			—	2		—	2
Sebastes rufus	Bank rockfish	—		1		1	1	3
Sebastes semicinctus	Halfbanded rockfish			—	—	2		2

contained up to 16 rockfish species; 73% of the samples contained five or more species. Samples ranging between 251–366 m in depth had up to 13 rockfish species with 52% of the samples having 5 or more species. Rockfish diversity declined at the deepest sites (~366 m).

Species assemblages

A total of 1,468 multispecies hauls were pooled together into a multi-survey, "All Years" analysis. Of the 20 rockfish species examined, 10 were identified as belonging to one of three groups or assemblages. Table 3 lists the results of RGA. The results of CA are shown in Figure 5 and summarized in Table 4. Group 1 consisted of shortspine thornyhead, Pacific ocean perch, darkblotched rockfish, and splitnose rockfish, *S. diploproa*. These four species occurred together in 200 samples at an average depth of 247 m (range=141–366 m). The mean rockfish CPUE in these hauls was 45.8 kg/ha of which the assemblage accounted for 82% of the total. Group 2 consisted of canary, yellowtail, and greenstriped rockfish. It also occurred in 200 survey hauls that averaged 150 m in depth (range= 91–291 m). Rockfish catches in hauls containing this assemblage were greater than Group 1, averaging 88.8 kg/ha. Canary, yellowtail, and greenstriped rockfish accounted for about 56% of the total rockfish CPUE at these sites. Group 3 consisted of sharpchin, redstripe, and rosethorn rockfish. This group was present in 99 samples. Its depth range

Table 2

Number of rockfish species (Scorpaenidae) from the west coast triennial groundfish surveys (1977–92) by depth interval in the Columbia and U.S.-Vancouver areas.

	Number of hauls per depth interval (m)						
Number of species	55–100	101–150	151–200	201–250	251–300	301–366	55–366
0	242	124	16	6	5	5	398
1	111	115	12	4	4	4	250
2	33	123	20	3	5	5	189
3	35	123	35	10	3	7	213
4	6	94	42	10	9	8	169
5	5	63	53	14	15	15	165
6	2	44	33	24	14	18	135
7	3	21	32	19	12	12	99
8	0	16	28	25	4	5	78
9	1	12	29	22	3	5	72
10	0	5	19	11	2	1	38
11	0	1	18	13	1	0	33
12	1	0	8	5	1	0	15
13	0	1	8	2	2	0	13
14	0	0	1	1	0	0	2
15	0	0	1	3	0	0	4
16	0	0	1	0	0	0	1
Total	439	742	356	172	80	85	1874

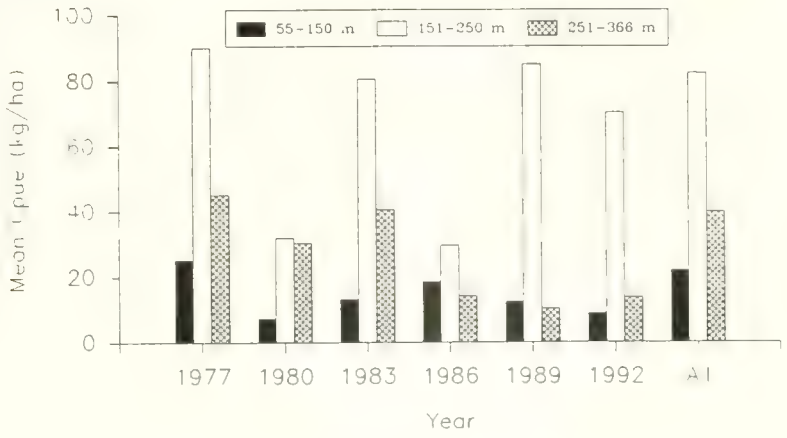

Figure 3

Relative abundance of rockfish (Scorpaenidae) expressed as mean catch per unit of effort (CPUE) for selected depth intervals by survey and for all surveys combined.

overlapped that of Group 2, 99–293 m, but this group was present, on average, in slightly deeper waters, 175 m (Fig. 6). Catches of this assemblage seemed to be more localized than were the others, occurring mainly in areas of highly irregular or hard bottom. Catch rates were highest at sites where this assemblage was present, averaging 159 kg/ha of which these three species accounted for 79% of the total. Shortbelly and pygmy rockfish, *S. wilsoni*, were also grouped together based on very low occurrences, probably an artifact of the grouping process.

The groupings assigned by the RGA and CA techniques were indentical except for two species. These were the assignment of redbanded rockfish to Group 1 by RGA only; and the assignment of greenstriped rockfish to Group 3 by RGA and Group 2 by CA.

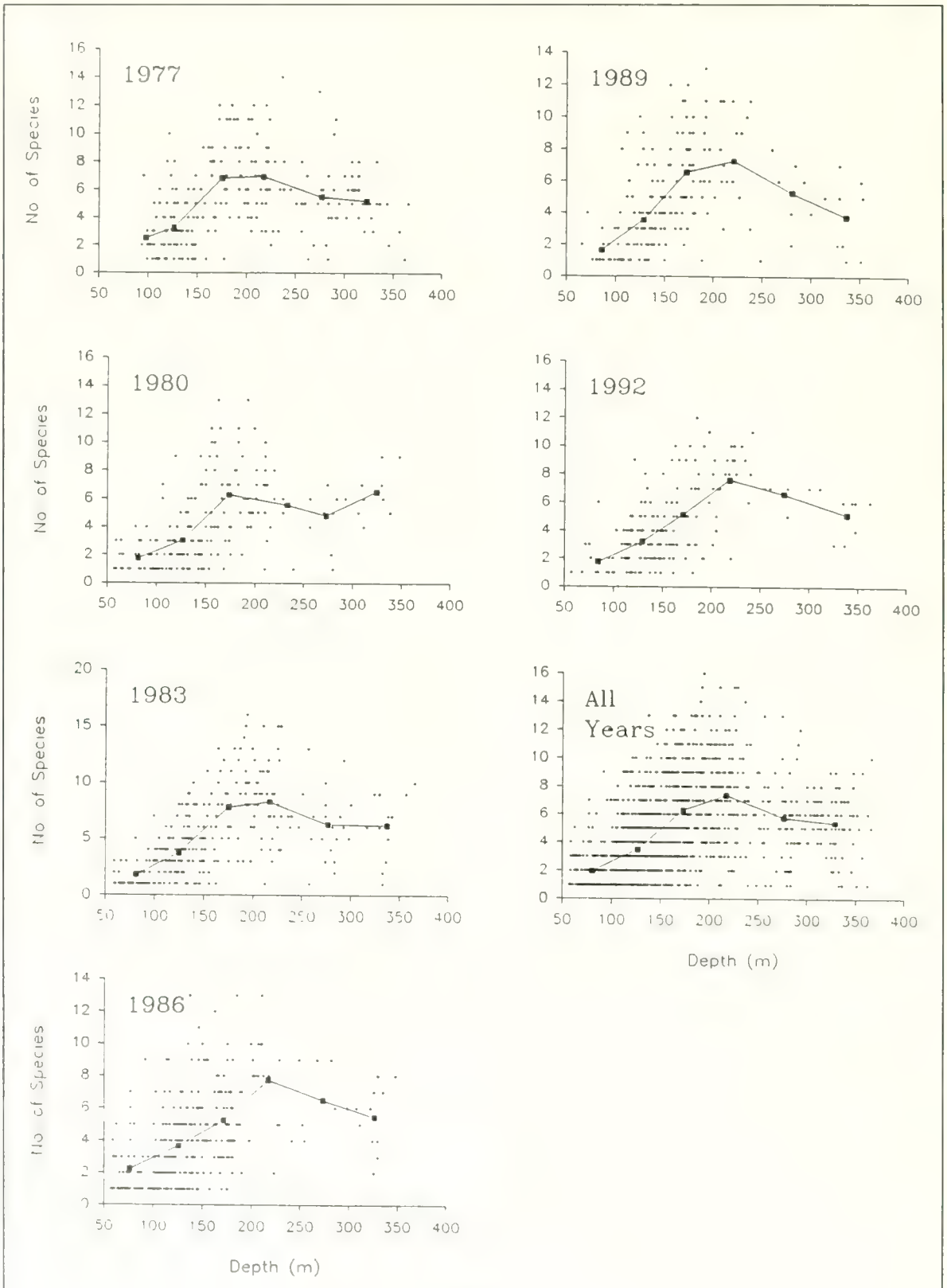

Figure 4

Number of rockfish species (Scorpaenidae) per tow (dots) and averaged over 55–100, 101–150, 151–200, 201–250, 251–300, and 301–366 m depth intervals (squares).

Table 3

Major species groups (1–3) of rockfish (Scorpaenidae) determined by recurrent group analysis by survey and for all surveys combined. Depth (m) and catch per unit of effort (CPUE, kg/ha) statistics refer to samples when all species listed in the group cooccurred. The group mean catch is also presented as the percent of the total average rockfish catch in those hauls. See Table 1 for scientific names.

Species	1977	1980	1983	1986	1989	1992	All years
Shortspine thornyhead	1	1	1	1	1	1	1
Pacific ocean perch	1	1	1	1	—	1	1
Splitnose rockfish	1	1	1	1	1	1	1
Darkblotched rockfish	1	—	1	1	1	2	1
Redbanded rockfish	1	1		—	1	1	1
Canary rockfish	2	2	2	2	3	—	2
Yellowtail rockfish	2	—	2	2	—	2	2
Greenstriped rockfish	2	2	1	3	3	2	3
Sharpchin rockfish	3	3	3	3	3	3	3
Rosethorn rockfish	3	3	3	3	3	3	3
Redstripe rockfish	—	—	3	—	—	3	3

Depth and catch statistics	Group 1	Group 2	Group 3
1977			
Occurrences	41	34	31
Mean depth (range)	255 (155–344)	163 (104–291)	217 (108–315)
Mean group CPUE (range)	48.7 (6.2–496.0)	57.6 (1.3–599.4)	11.2 (0.2–72.4)
Proportion of total CPUE (%)	79.8	63.5	9.5
1980			
Occurrences	19	37	24
Mean depth (range)	249 (150–338)	154 (82–274)	195 (144–348)
Mean group CPUE (range)	39.7 (0.9–155.7)	14.0 (0.2–116.7)	11.2 (0.1–94.4)
Proportion of total CPUE (%)	73.6	23.6	13.1
1983			
Occurrences	31	80	26
Mean depth (range)	213 (154–293)	143 (59–251)	196 (124–293)
Mean group CPUE (range)	32.2 (1.7–126.0)	36.1 (0.6–742.5)	71.1 (0.1–681.8)
Proportion of total CPUE (%)	67.9	47.1	34.5
1986			
Occurrences	31	73	34
Mean depth (range)	233 (150–348)	124 (59–185)	165 (97–267)
Mean group CPUE (range)	37.3 (1.5–417.8)	48.0 (0.1–745.3)	9.2 (0.3–87.4)
Proportion of total CPUE (%)	89.2	79.7	15.8
1989			
Occurrences	27	–	22
Mean depth (range)	230 (132–353)	–	174 (112–238)
Mean group CPUE (range)	9.8 (0.3–64.8)	–	22.7 (0.6–92.4)
Proportion of total CPUE (%)	36.3	—	23.3
1992			
Occurrences	9	24	15
Mean depth (range)	230 (214–260)	155 (119–219)	167 (113–223)
Mean group CPUE (range)	31.0 (7.9–98.8)	25.6 (1.3–283.3)	120.8 (0.7–533.4)
Proportion of total CPUE (%)	53.5	76.2	67.3
All years			
Occurrences	135	278	89
Mean depth (range)	259 (155–366)	141 (59–291)	173 (97–293)
Mean group CPUE (range)	45.9 (1.7–496.0)	53.3 (0.1–1205.2)	26.1 (0.3–684.7)
Proportion of total CPUE (%)	80.3	62.8	12.5

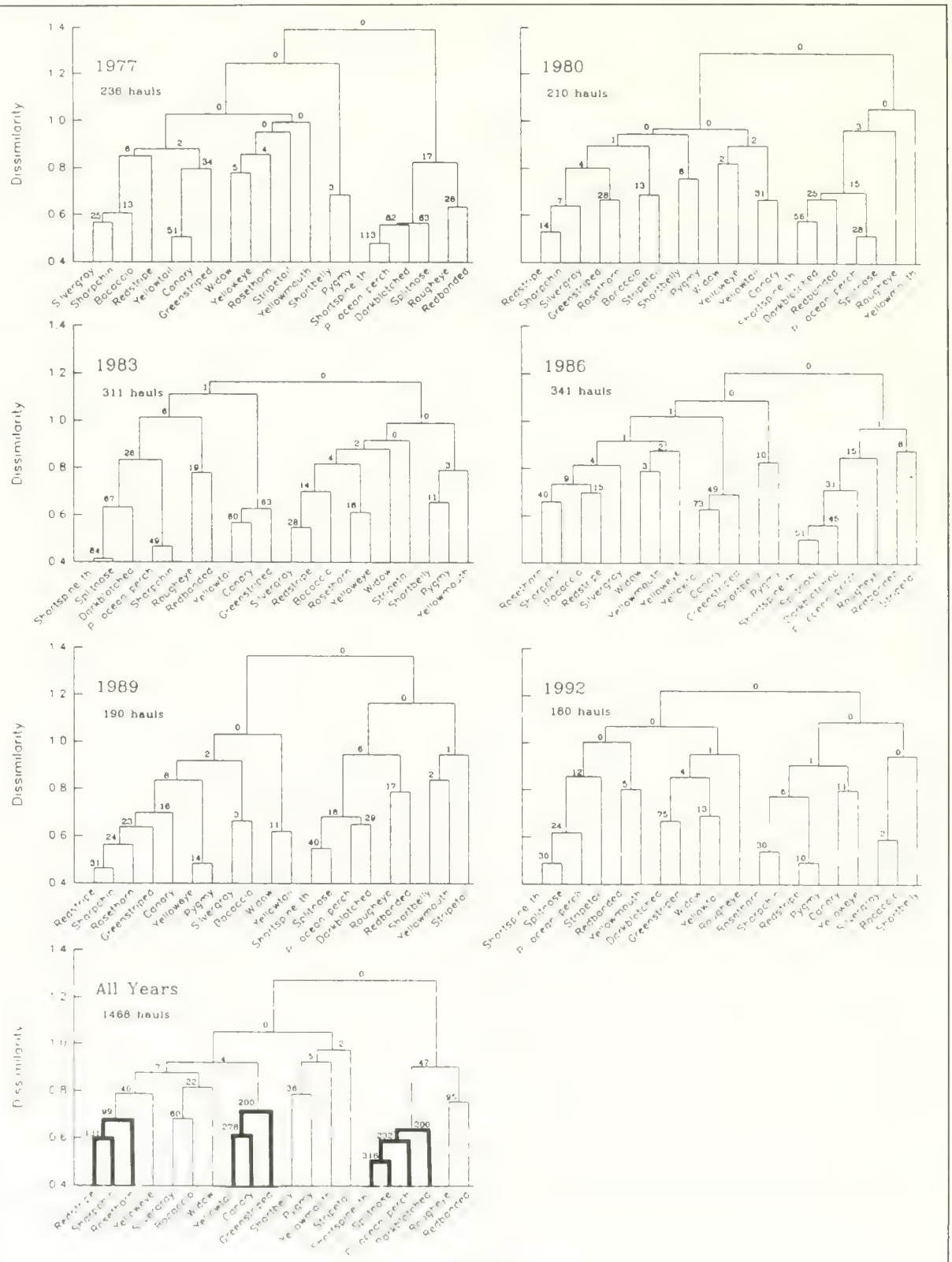

Figure 5

Dendrograms showing the relationships among rockfish (Scorpaenidae) species and assemblages (in bold) in the Columbia and U.S.-Vancouver areas. The values on top of each cluster correspond to its frequency of occurrence with all members present.

Table 4

Catch per unit of effort (CPUE) and depth (m) data from the combined 1977–92 west coast triennial groundfish surveys presented for the three rockfish (Scorpaenidae) assemblages identified by cluster analysis. The species catch composition data (listed across) are from hauls containing these assemblages and include mean CPUE (kg/ha) and standard deviation; the percentage of the total rockfish CPUE taken in these hauls, and the percent frequency of occurrence. Values below 0.1 are indicated by the letter *t*. Differences in totals are a result of rounding. See Table 1 for scientific names.

All years (1977–92)	Group 1				Group 2				Group 3			
Total hauls[1]	200				200				99			
Mean depth (range)	247 (141–366)				150 (91–291)				175 (99–293)			
Mean CPUE	45.8				88.8				158.6			
Catch composition	Mean CPUE	SD	% CPUE	% Occur.	Mean CPUE	SD	% CPUE	% Occur.	Mean CPUE	SD	% CPUE	% Occur.
Group 1												
Darkblotched	9.0	2.26	19.7	100.0	1.4	0.27	1.6	52.0	0.5	0.22	0.3	22.2
Pacific ocean perch	17.6	3.06	38.4	100.0	2.9	1.03	3.4	26.0	9.6	3.14	6.1	53.5
Shortspine thornyhead	3.8	0.29	8.4	100.0	0.5	0.13	0.5	37.5	0.7	0.16	0.4	46.4
Splitnose	7.0	1.03	15.4	100.0	0.3	0.10	0.3	21.0	1.1	0.42	0.7	26.3
Total	37.4		81.9		5.2		5.8		12.0		7.5	
Group 2												
Canary	0.4	0.14	0.9	25.5	15.4	4.03	17.3	100.0	16.8	5.59	10.6	66.7
Greenstriped	0.6	*t*	1.3	48.0	2.7	0.33	3.0	100.0	3.9	0.59	2.4	89.9
Yellowtail	0.6	0.19	1.3	19.0	31.2	6.18	35.1	100.0	24.3	7.39	15.3	50.5
Total	1.6		3.5		49.2		55.5		44.9		28.3	
Group 3												
Redstripe	*t*	*t*	0.2	8.0	14.1	4.10	15.9	33.5	46.1	10.28	29.1	100.0
Rosethorn	0.2	*t*	0.4	34.0	0.6	0.14	0.7	40.5	1.9	0.26	1.2	100.0
Sharpchin	3.0	0.78	6.7	43.5	9.8	3.91	11.1	39.5	31.1	8.36	19.6	100.0
Total	3.2		7.3		24.5		27.6		79.1		49.9	
Other rockfish												
Bocaccio	0.3	*t*	0.6	16.5	1.5	0.34	1.7	37.0	2.5	0.68	1.6	42.4
Pygmy	*t*	*t*	*t*	3.0	0.5	0.27	0.6	14.0	3.4	1.52	2.2	31.3
Redbanded	0.8	0.12	1.7	67.5	0.6	0.29	0.7	14.0	0.4	0.16	0.3	28.3
Rougheye	0.5	0.12	1.1	31.5	0.2	*t*	0.2	9.5	*t*	*t*	*t*	7.1
Shortbelly	*t*	*t*	0.2	8.5	0.3	0.14	0.3	18.5	0.7	0.34	0.4	24.2
Silvergray	0.4	0.20	0.9	10.5	1.6	0.38	1.9	25.5	8.8	5.18	5.5	45.4
Stripetail	0.3	*t*	0.7	31.0	0.3	*t*	0.3	17.0	0.5	0.17	0.3	31.3
Widow	0.4	0.19	0.9	23.5	3.4	1.66	3.9	25.5	3.1	1.73	2.0	27.3
Yelloweye	*t*	*t*	0.2	3.0	1.1	0.39	1.2	20.0	1.7	0.69	1.1	40.4
Yellowmouth	*t*	*t*	0.2	3.5	0.1	*t*	0.1	4.0	1.1	0.49	0.7	16.2
Remaining rockfish	0.4		0.5		0.2		0.2		0.3		0.2	
Total	3.4		7.2		9.8		11.1		22.5		14.3	

[1] Includes 18 hauls having both Groups 1 and 2; 11 hauls having both Groups 1 and 3, and 36 hauls having both Groups 2 and 3.

In addition to the "All Years" analysis, individual surveys were classified, revealing moderate agreement among surveys. Of the two methods, RGA (presence-absence) produced more consistent results across individual surveys. Changes in the structure of the three assemblages in any given year usually involved the addition or omission of one species or the shifting of one of the more ubiquitous species into another group.

On the other hand, assemblage patterns across surveys were less discernible with the biomass-oriented CA because of the high variability in rockfish CPUE's, particularly among shelf species. Usually, at the highest dissimilarity level (Fig. 5), CA partitioned the offshore community into a deep water, upper-slope group and a shallower water, mid-shelf group. The deeper species consisted of shortspine thornyhead, Pacific ocean perch, darkblotched rockfish, and splitnose rockfish. Two additional species, redbanded and rougheye, *S. aleutianus*, rockfish, were often closely associated with this group. In 1983, sharpchin, *S. zacentrus*, rockfish was included. The shallower species comprised two core assemblages (most easily seen in the "All Years" dendrogram). The first of these consisted of canary, yellowtail, and to a lesser extent, greenstriped rockfish. This assemblage was clearly identified from 1977 through 1986. However, in 1989 and 1992, it was not defined, most likely because of the shift in survey design that de-emphasized canary and yellowtail rockfish as target species, thus reducing the sampling effort in areas where they were most likely to have been found together. The other core assemblage among shelf rockfishes consisted of sharpchin, rosethorn, and redstripe rockfish, *S. proriger*. However, since these species were taken along with a variety of other species, such as silvergray rockfish, bocaccio, *S. paucispinis*, yelloweye, *S. ruberrimus*, canary, and yellowtail rockfish, CA dendrograms showed considerable variability between years.

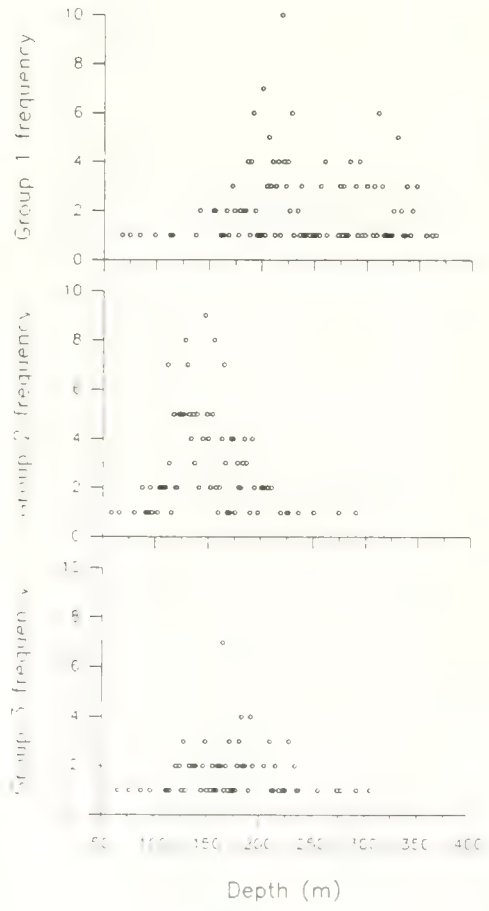

Figure 6

The frequency of occurrence by depth of the three rockfish assemblages determined from cluster analysis. Group 1 consists of shortspine thornyhead, Pacific ocean perch, darkblotched rockfish, and splitnose rockfish. Group 2 consists of yellowtail, canary, and greenstriped rockfish. Group 3 consists of sharpchin, redstripe, and rosethorn rockfish. See Table 1 for scientific names.

Discussion

Survey data have provided the unique opportunity to study broad-scale community composition of offshore rockfishes, including smaller specimens typically discarded in commercial operations. These data are useful to both ecologists interested in describing the biological associations of our ocean's resources and to resource managers concerned with commercial catch and bycatch issues.

For a variety of reasons however, survey-defined assemblages may differ from assemblages determined through commercial fisheries data. Most of these revolve around the strict adherence to scientific design of most surveys as opposed to industry's opportunistic approach driven by economic needs. For example, the assemblages identified in this study would probably not be detected if sampling were limited to catches made while targeting strong hydroacoustic signals (Richards et al., 1991). Pelagic and semipelagic aggregations, such as widow, shortbelly, and in some cases yellowtail rockfish are under-represented in this study because they were sampled less intensively during the surveys. Differences in catch composition is also gear dependent. Our survey gear and methods of deployment were standard-

ized to facilitate comparisons among surveys. The trawl employed a 89-mm mesh codend with a 32-mm liner, capable of retaining juveniles and smaller-sized species, such as rosethorn and greenstriped rockfish. Smaller species may not be caught in similar proportions in commercial catches.

On the other hand, fishermen select, modify, and operate their gear based on fishing strategy. These strategies have changed over the years to adapt to reduced allowable harvests and the imposed vessel trip limits. To economize, fishermen target several species over the course of a single trip, using more than one type of gear (Tagart[5]). For example, a vessel may begin using midwater gear directed at catching a limit of widow rockfish, then switch to bottom gear to target on yellowtail rockfish. Once the trip limits for these two species are reached, the captain may opt to fish flatfish or change to a more generalized rockfish strategy keeping larger specimens of darkblotched, silvergray, redstripe, or sharpchin rockfish.

Because survey and fishery tactics differ greatly, I assessed whether the assemblages found to persist in summer surveys based on systematic sampling also occurred in commercial collections characterized by opportunistic sampling, market conditions, and management-imposed restrictions. The literature referred to previously describes various west coast fish assemblages determined from different sampling techniques, classification methods, and data types. Although none of these studies used a time-series of this duration, Rogers and Pikitch (1992) identified two rockfish assemblages using year-round (1985–87), prediscard, commercial trawl data from off the coasts of Oregon and Washington. Briefly, they examined five fishing strategies, one of which targeted demersal rockfishes using bottom trawl gear. Even though the survey depth range was narrower than that of the commercial operations, the results of Rogers and Pikitch (1992) share much in common with the present study. Both studies describe an assemblage of deepwater rockfishes with three species in common: Pacific ocean perch, darkblotched rockfish, and splitnose rockfish. The present study also includes shortspine thornyhead, whereas Roger and Pikitch (1992) include sharpchin and yellowmouth rockfish.[6] Their second rockfish assemblage combined bocaccio, yellowtail, canary, yelloweye, and sharpchin rockfish, species assigned to either one of two separate assemblages or caught too inconsistently to be considered part of any assemblage in the present study.

Rogers and Pikitch (1992) included in their analysis 11 of the 20 scorpaenids that I examined. These were selected based on either an arbitrarily determined weight threshold (1% of the total commercial catch from all five fishing strategies) or if fishermen claimed to target a species (e.g. bocaccio and yelloweye rockfish). Most of those selected represented larger proportions of the commercial catch; however, other rockfishes were continuously affected by trawling. When classifying assembages based on biomass data, one takes the risk of failing to recognize a less abundant member of the community. In the study by Rogers and Pikitch (1992), several minor rockfish species were overshadowed by catches of the area's dominant species. Nearly 60% of the total catch sampled from all fishing strategies combined was nonrockfish. Among the rockfishes, widow rockfish accounted for the highest percentage (15%) of the sample catch, about 75% of which was taken by midwater trawl (Rogers[7]). Assuming that the data from their study is representative of commercial operations, we can infer the impact that trawling has on the overall rockfish community, including the minor species, by examining prediscard catch data from hauls where bottom rockfish were targeted (i.e. bottom rockfish fishing strategy). In these data, nonrockfish composed only 20% of the catch whereas widow rockfish, taken by bottom trawl, still accounted for 15% of the strategy's total. Of the species assemblages identified in the present study, yellowtail, canary, and greenstriped rockfish accounted for 30% of the total; shortspine thornyhead, Pacific ocean perch, darkblotched rockfish, and splitnose rockfish accounted for 13%; and sharpchin, redstripe, and rosethorn rockfish accounted for 10% of the total catch. Large marketable species typically seen in the landings, like bocaccio, silvergray rockfish, and yelloweye rockfish, composed only 4% of the prediscard catch.

Conclusion

The separation of deepwater species from shelf species supports the division of the "*Sebastes* complex" management category into smaller units of greater ecological consequence, as also suggested by Rogers and Pikitch (1992). There is enough variability, however, in the catches of shelf rockfish, as characterized by the relatively high levels of dissimilarity among groupings (Fig. 5), to warrant the use of caution when designating assemblages. While this study recognized two assemblages of shelf species vulner-

[5] Tagart, J. Washington Dept. Fish., Olympia, WA 98504-3144. Personal commun., April 1991.

[6] For unknown reasons, fishery data had substantially greater abundance of yellowmouth rockfish than did the survey data.

[7] Rogers, J. B. Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., Tiburon, CA 94920. Personal commun., Nov. 1993.

able to bottom trawling off Oregon and Washington, a resource manager may elect to base management decisions on the union of these two because of the difficulty in monitoring the often discarded sharpchin-redstripe-rosethorn rockfish assemblage. However, in managing the rockfish community as a whole, this assemblage needs to be considered along with other minor species commonly caught in the fishery.

Our understanding of the associations among rockfish has improved greatly. Assemblage studies, combined with studies on life history, distribution, and abundance, continue to assist in refining current resource management policies and may eventually lead to a more multispecies management approach. Such an approach will address the impact on the ecosystem when operations target on a single species, such as yellowtail rockfish, with little regard to the effects on other species, particularly those of lower economic value. Likewise, it will also address the continued removal of a species like yellowtail rockfish due to incidental catch when operations target on another species.

Acknowledgments

Fisheries biologists must often endure the harsh marine environment for extended periods of time, forsaking the more comfortable conditions of their offices and homes. I thank all of the participants, scientists, and crews of the NMFS west coast triennial surveys. Gary Walters was responsible for bringing the cluster analysis program to the AFSC and provided guidance for its use. Mark Wilkins realized this study's benefits and enabled my escape from many routine exercises to complete this work. I am also most grateful to my reviewers, particularly those who witnessed the evolution of this paper.

Literature cited

Bray, J. R., and J. T. Curtis.
1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:325–349.

Clifford, H. T., and W. Stephenson.
1975. An introduction to numerical classification. Academic Press, Inc., NY, 229 p.

Coleman, B. A.
1986. The 1980 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, length and age composition. NOAA Tech. Memo. NMFS-F/NWC–100, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 181 p.

Coleman, B. A.
1988. The 1986 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, length and age composition. NOAA Tech. Memo. NMFS-F/NWC-152, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 145 p.

Eschmeyer, W. N., and E. S. Herald.
1983. A field guide to Pacific coast fishes of North America. Houghton Mifflin, Boston, 336 p.

Fager, E. W., and J. A. McGowan.
1963. Zooplankton species groups in the North Pacific. Science 140:453–460.

Gabriel, W. L.
1982. Structure and dynamics of northeastern Pacific demersal fish assemblages. Ph.D. diss., Oregon State Univ., Corvallis, 298 p.

Gunderson, D. R., and T. M. Sample.
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42(3–4):2–16.

Lance, G. N., and W. T. Williams.
1967. A general theory of classificatory sorting strategies. I: Hierarchical systems. Comput. J. 1:15–20.

Nagtegaal, D. A.
1983. Identification and description of assemblages of some commercially important rockfishes (*Sebastes* spp.) off British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. Vol. 1, 82 p.

Richards, L. J., R. Kieser, T. J. Mulligan, and J. R. Candy.
1991. Classification of fish assemblages based on echo integration surveys. Can. J. Fish. Aquat. Sci. 48:1264–1272.

Rogers, J. B., and E. K. Pikitch.
1992. Numerical definition of groundfish assemblages caught off the coasts of Oregon and Washington using commercial fishing strategies. Can. J. Fish. Aquat. Sci. 49:2648–2656.

Weinberg, K. L., M. E. Wilkins, and T. A. Dark.
1984. The 1983 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, age and length composition. NOAA Tech Memo. NMFS-F/NWC-70, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 376 p.

Weinberg, K. L., M. E. Wilkins, R. R. Lauth, and P. A. Raymore Jr.
1994. The 1989 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, and length and age composition. NOAA Tech Memo. NMFS-AFSC-33, Alaska Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, WA 98115-0070, 168 p.

Results of long-term, seasonal sampling for *Penaeus* postlarvae at Breach Inlet, South Carolina

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Recruitment of postlarvae of commercially important penaeid shrimp has been studied in several areas in the southeastern United States, e.g. on the Atlantic coast (Bearden, 1961; Williams and Deubler, 1968; Williams, 1969; Allen et al., 1980) and the Gulf of Mexico (Baxter, 1963; George, 1962; Loesch, 1965; Christmas et al., 1966; Baxter and Renfro, 1967; Caillouet et al., 1968, 1970; Ford and St. Amant, 1971). Findings from these studies indicate that postlarvae are generally concentrated near oceanic inlets, different species are abundant at different times of the year, ingress through inlets into estuarine nursery areas is often influenced by factors such as tide and time of day, and correlations between number of postlarvae and subsequent commercial landings is often poor.

In South Carolina most published studies have examined postlarval recruitment over a one- to two-year period (Bearden, 1961; Olmi, 1986; Wenner and Beatty, 1993). Long-term sampling was conducted by Lunz[1] at several coastal sites in South Carolina in an effort to predict subsequent commercial harvest. As an extension of this work, long-term, seasonal sampling was conducted at a single site near Charleston, South Carolina, to determine relative abundance and timing of recruitment of *Penaeus* postlarvae. This study is part of a continuing effort to relate postlarval abundance to subsequent landings and to evaluate spawning success of parental stocks.

Materials and methods

Samples were collected with a 1-m diameter, 500-µm mesh plankton net fitted with a flowmeter at Breach Inlet, South Carolina (between Sullivan's Island and the Isle of Palms), from January 1975 to August 1992 (Fig. 1). Breach Inlet is an oceanic inlet with high velocity tidal currents (up to 150 cm/sec flow). The tides in South Carolina are semidiurnal and have an average range of tidal height of approximately 2 m between mean low water and mean high water. Breach Inlet was chosen as a site for intensive monitoring of recruitment because of its accessibility (boats are not required for sampling and it can be sampled in inclement weather). Preliminary studies have shown that postlarvae can be collected in consistently high numbers (several hundred per sample) at Breach Inlet, and catches are comparable to collections made in other estuaries in South Carolina (J. Whitaker, unpubl. data).

The net was deployed from a bridge over the inlet and fished near the bottom (approx. 10 m depth) for two one-hour periods during daylight flood tides. Prior to 1978, paired samples were taken twice weekly (approximately 30 minutes elapsed between samples). This effort was greatly reduced when abundance of postlarval brown shrimp, *Penaeus aztecus*, could not be correlated with commercial landings. After 1977, regular sampling involved collecting two unpaired samples per tide at one or two week intervals from late January to early August. Hydrographic information, including water temperature and salinity, were also collected during sampling (Table 1).

In addition to bottom daylight samples, consecutive samples were taken over a full tidal cycle during day and night (two surface and two bottom samples per tide) in some years during periods of high abundance to examine possible influences of tide, time of day, and location of the net on postlarval catch rates. Consecutive samples of *P. aztecus* were collected on 12–13 March 1975, 26–27 February and 30–31 March 1976, 17–18 March 1977, 24–25 February and 10–11 March 1983, 2–3 March and 2–3 April 1985, and 21 February and 3–4 March 1986 (flood tide only in 1986). Consecutive samples for *P. setiferus* were collected on 9–10 June and 16–17 July 1975, 27–28 May and 28–29 June 1976, 9–10 June 1983, and 29–30 May 1989 (flood tide only in 1989).

Plankton samples were preserved in 10% buffered formalin-seawater and sorted in the laboratory. Postlarvae were sorted to species in most instances by using characteristics identified by Pearson (1939), Williams (1959), and

Contribution 335 of the South Carolina Marine Resources Center.

[1] Lunz, G. R. 1965. Annual report 1963–64, Bears Bluff Laboratories. Contrib. Bears Bluff Lab. No. 41, 10 p.

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Fishery Bulletin 92:633–640 (1994).

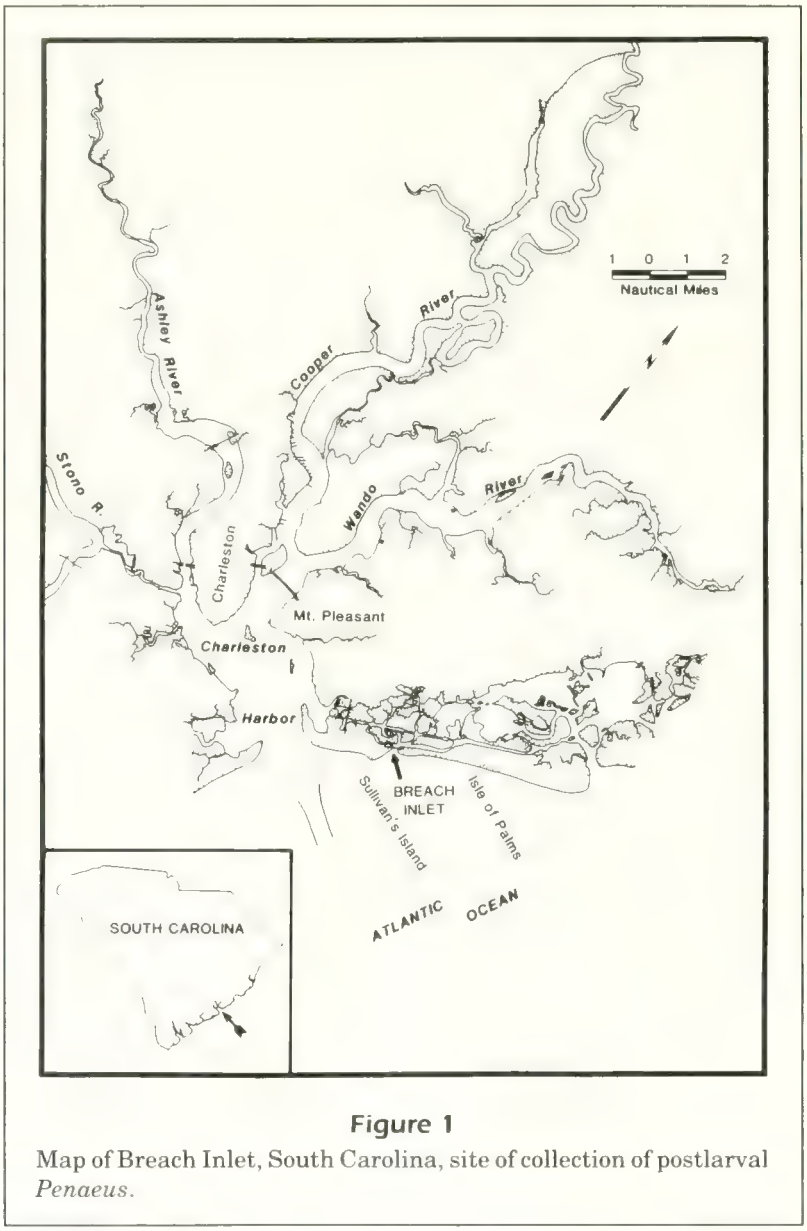

Figure 1

Map of Breach Inlet, South Carolina, site of collection of postlarval *Penaeus*.

Ringo and Zamora (1968). Postlarvae with overlapping characters were identified to genus.

Counts of postlarvae were converted to density (numbers per 1,000 m^3). Preliminary analyses revealed these data to be nonnormal and with large variation; therefore, potential effects of time of day, tidal stage, and location of nets (surface versus bottom) on ingress of postlarvae collected by consecutive sampling were tested with the nonparametric Mann-Whitney test on densities of postlarvae (flood tide only for time of day and location of nets; Siegel, 1956). The effect of lunar phase on catches made during regular sampling (daytime bottom collections made on flood tide during season of peak abundance) was tested with the nonparametric Kruskal-Wallis test on densities grouped by four lunar periods (new, full, first, or last quarter) pooled from the entire year's data (Siegel, 1956). Differences among groups were considered statistically significant at the $P \leq 0.05$ level. The above data were log-transformed to facilitate graphic representation of means and standard deviations (Figs. 2 and 3). An annual index of abundance ($\Sigma \log((\text{number}/1{,}000 m^3) + 1)/\text{number of samples}$); Elliot, 1977) was calculated for each species for use in regression analysis. The index was computed from February, once densities reached 20/1,000 m^3, through April for *P. aztecus*, and from May through August for *P. setiferus*. Annual indices of postlarval abundance were regressed against annual estimates of harvest to ascertain possible relation-

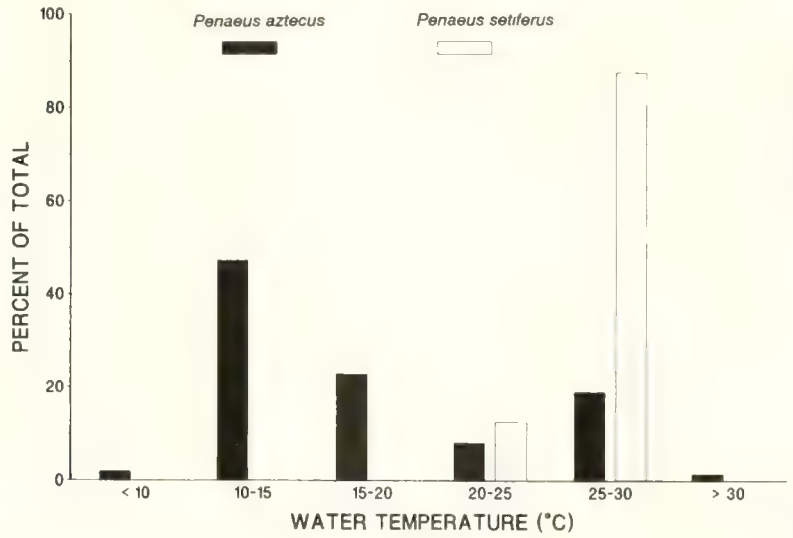

Figure 2

Distribution of catch of postlarval penaeid shrimp, *Penaeus aztecus* and *Penaeus setiferus*, over the range of water temperature observed at Breach Inlet during regular sampling.

ships.[2] Numbers of shrimp landed each year were estimated by multiplying landed weight by average grade (average number of shrimp per kg).

Results

A total of 102,109 *Penaeus* postlarvae were collected from 7 January 1975 to 3 August 1992 at Breach Inlet. Of the total catch, 68.3% were identified as brown shrimp, *P. aztecus*, 23.3% as white shrimp, *P. setiferus*, and 0.8% as pink shrimp, *P. duorarum*. The remaining 7.6% were identifed as *Penaeus* spp. The majority of the latter category were tentatively identified as *P. aztecus*, and were collected primarily from late May through July. Because *P. duorarum* postlarvae were collected in relatively low numbers and some uncertainty exists with identification, the analysis includes only *P.aztecus* and *P. setiferus*.

The majority of *P. aztecus* postlarvae were collected between February and April, when water temperature was between 10 and 20°C (the catch peaked between 12° and 16°C). *Penaeus setiferus* was collected only when temperatures exceeded 20°C; most were taken at temperatures between 25 and 30°C (peak abundance occurred in June; Fig. 2). Samples of *P. aztecus* averaged several hundred individuals in each year during times of peak ingress. However, catches of *P. setiferus* were much more variable, averaging zero in some years and several hundred in years of high abundance (Table 2).

Consecutive sampling conducted day and night on both ebb and flood tides revealed that both species

Table 1

Average and range of bottom water temperature and salinity observed at Breach Inlet, South Carolina and number of samples of *Penaeus* postlarvae collected during regular sampling, 1975–92.

Year	Temperature (°C)	Salinity (ppt)	Number of samples
1975	20.2 (9.3–29.4)	28.6 (15.0–35.0)	256
1976	19.4 (7.0–30.0)	30.7 (26.0–35.0)	236
1977	21.4 (4.9–32.1)	31.5 (21.0–36.0)	244
1978	21.2 (5.9–31.5)	29.8 (18.0–35.0)	117
1979	18.8 (6.7–28.2)	28.8 (24.0–35.0)	57
1980	15.3 (5.7–25.6)	28.8 (20.0–34.0)	34
1981	18.3 (10.9–31.0)	32.4 (25.0–36.0)	46
1982	18.9 (9.5–28.1)	28.5 (22.0–32.0)	22
1983	14.9 (8.1–26.2)	27.6 (18.0–32.0)	33
1984	23.7 (8.1–30.5)	29.0 (23.0–34.0)	63
1985	21.8 (11.3–30.7)	31.7 (26.0–36.0)	48
1986	20.8 (9.1–30.0)	31.1 (27.0–34.0)	36
1987	17.4 (8.0–29.2)	32.1 (26.0–36.0)	36
1988	19.4 (11.2–30.5)	29.1 (21.0–35.0)	38
1989	20.8 (10.5–30.6)	32.7 (26.0–36.0)	48
1990	21.3 (11.9–30.1)	31.1 (25.0–35.0)	42
1991	20.2 (10.4–29.4)	29.4 (21.0–35.0)	36
1992	21.3 (9.3–30.1)	29.1 (24.0–33.0)	34

[2] Low, R. A. 1992. Survey of the South Carolina Shrimp baiting fishery, 1991. South Carolina Marine Res. Cent. Data Rep. 9, 29 p.

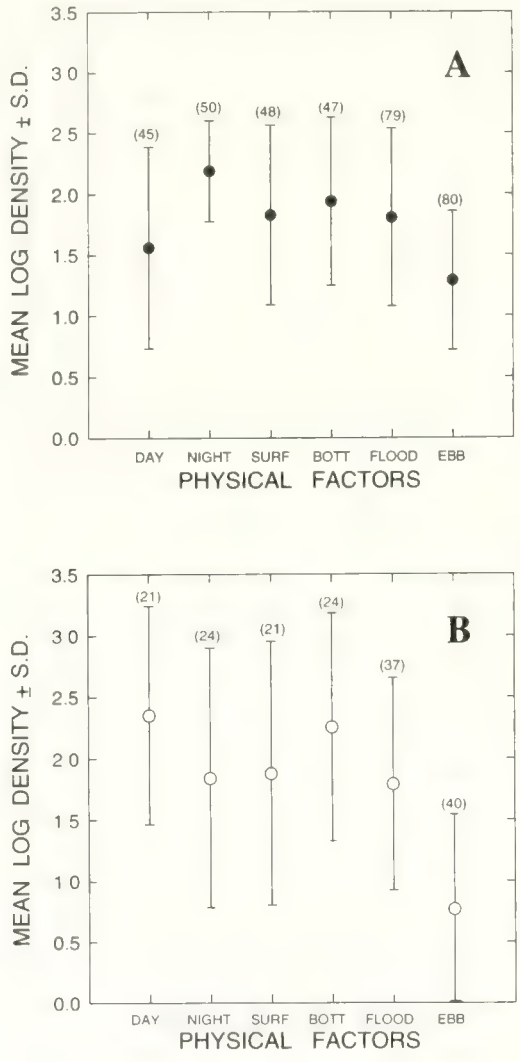

Figure 3

Mean density of postlarval penaeid shrimp (**A**) *Penaeus aztecus* and (**B**) *Penaeus setiferus* grouped by time of day, tide, and location of net at Breach Inlet, South Carolina. Samples were collected over 24-hour periods during times of peak abundance. Log Density= log((number/1,000m^3) + 1). SD=standard deviation. Numbers in parenthesis=number of samples. Surf=surface, Bott=bottom.

were significantly more abundant in samples taken during flood tides than during ebb tides (P<0.001; Fig. 3). Significantly more *P. aztecus* were collected at night on flood tides ($\bar{x}$=228.7/1,000m^3) than during daylight flood tides ($\bar{x}$=147.4/1,000m^3; P<0.001), whereas no significant difference between catches made during day ($\bar{x}$=877.9/1,000m^3) versus night ($\bar{x}$=610.2/1,000m^3) were noted for *P. setiferus* (P=0.114; Fig. 3). No significant differences in catches were noted for either species when surface and bottom collections were compared (P=0.595 for *P. aztecus*; P=0.270 for *P. setiferus*; Fig. 3).

Significant differences among catches made by regular sampling grouped by lunar phase (new moon, first quarter, full moon, last quarter) were detected for both *P. aztecus* (P<0.0001) and *P. setiferus* (P<0.006). Fewest postlarvae of both species were collected during full moon phases; *P. aztecus* were more abundant during the last quarter than at other times (Fig. 4), whereas *P. setiferus* was most abundant during the first quarter.

Results of correlation analysis revealed a low correlation (r^2=0.03; P=0.523) between annual indices of abundance of postlarval *P. aztecus* and subsequent landings. A much higher correlation was obtained for *P. setiferus* (r^2=0.79; P<0.001; Fig. 5). The regression equation for estimated number of *P. setiferus* landed was $Y = 40.4 + 119.0X$ (Y=estimated number landed, X=annual index of postlarval abundance).

Discussion

Our results are generally similar to observations on *Penaeus* postlarvae made by others in the southeastern United States (including the Gulf of Mexico). *Penaeus aztecus* is most abundant in springtime at water temperatures comparable to the range of temperatures observed in this study (Bearden, 1961; Williams and Deubler, 1968; Allen et al., 1980). It has been postulated that the majority of brown shrimp postlarvae recruited in the spring are produced by spawning from the previous fall (Temple and Fischer, 1967; Aldrich et al., 1968; Anderson, 1970; Whitaker[3]). Ingress begins after nearshore water temperatures approach 12°C. In contrast, *Penaeus setiferus* postlarvae are recruited in spring and summer shortly after being spawned in adjacent oceanic waters (Pearson, 1939; Lindner and Anderson, 1956). When compared to overall catches of *P. setiferus*, *P. aztecus* have often been collected in greater abundance in South Carolina (Bearden, 1961; Lunz, 1965; Olmi, 1986; Wenner and Beatty, in press) and in Texas (Baxter and Renfro, 1967).

Prior studies have shown that *P. aztecus* postlarvae are often more abundant in nighttime collections and on high (flood) tides (Caillouet et al., 1970; Duronslet et al., 1972), similar to the pattern observed in this study. This is probably due to both increased nocturnal activity and decreased gear avoidance at night

[3] Whitaker, J. D. 1982. A possible mechanism for brown shrimp postlarval recruitment. Paper presented at South Carolina Fisheries Workers Assoc. annu. meet., Clemson, SC, 24–25 Feb. 1982. Unpubl. manuscr., 3 p.

Table 2

Mean density (number per 1,000m^3), standard deviation, and number of samples collected for brown shrimp, *Penaeus aztecus*, and white shrimp, *Penaeus setiferus*, postlarvae during season of peak ingress at Breach Inlet, South Carolina 1975–92.

	P. aztecus			*P. setiferus*		
Year	Mean	SD	*N*	Mean	SD	*N*
1975	149.9	185.21	98	78.3	265.13	124
1976	119.2	184.83	100	51.7	90.65	104
1977	75.4	105.53	72	0.0	0.00	136
1978	90.1	150.80	40	0.3	1.31	53
1979	86.1	123.80	28	48.5	84.33	25
1980	209.7	144.08	20	2.6	4.17	10
1981	81.1	124.45	26	0.0	0.00	18
1982	—	—	—	9.4	18.16	10
1983	291.2	417.26	13	3.8	6.19	6
1984	125.4	192.53	10	10.5	36.33	39
1985	68.7	101.65	18	2.7	7.35	24
1986	182.7	177.05	14	4.8	19.55	20
1987	58.3	37.38	13	24.7	55.61	14
1988	69.2	112.20	14	10.8	31.55	23
1989	95.2	83.52	20	671.2	1,627.30	25
1990	336.8	348.82	18	29.5	75.82	21
1991	132.1	170.84	18	351.6	452.27	16
1992	129.7	200.25	12	326.6	1,035.87	19

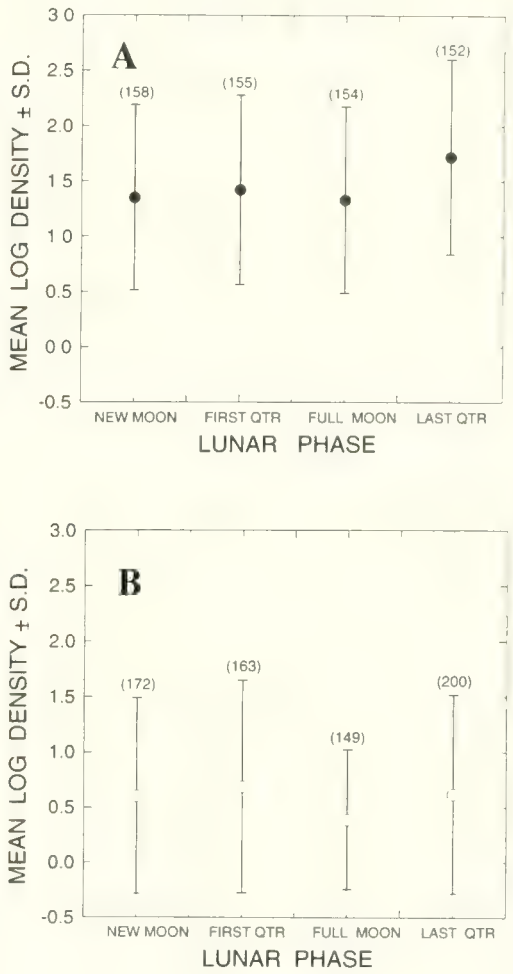

Figure 4

Mean density of postlarval penaeid shrimp (**A**) *Penaeus aztecus* and (**B**) *Penaeus setiferus* grouped by lunar phase during months of peak abundance at Breach Inlet. Samples collected near the bottom on flood tide during daylight (regular sampling). Log Density=log ((number/1,000 m^3) + 1). SD=standard deviation. Qtr=quarter. Numbers in parenthesis=number of samples.

(Williams and Deubler, 1968; Matthews et al., 1991). Olmi (1986) in addition to collecting more *P. aztecus* at night, also collected the majority of *P. setiferus* postlarvae at night in a tidal creek in South Carolina. These findings are in agreement with similar studies in the Gulf of Mexico, where *P. setiferus* was found to be more abundant near the surface at night in an inlet (Duronslet et al., 1972) and over a tidal flat (Caillouet et al., 1968). Wenner and Beatty (1993) collected 95% of all penaeid postlarvae at night (including a collection at a creek adjacent to Breach Inlet). In our study, no difference was detected between day and night catches of *P. setiferus*, possibly because we employed a larger net than in the other studies conducted in South Carolina in a higher-velocity tidal flow. This may have minimized avoidance of the gear by postlarvae during daylight. Additional sampling may clarify these observations.

Similar to observations made in our study, Olmi (1986) generally collected fewer postlarvae during full moon phases in South Carolina. Williams and Deubler (1968) in North Carolina and Allen et al. (1980) in the Florida Keys collected fewer *P. duorarum* at night during full moon phases than during new moon phases. Perhaps high light levels at night may delay ingress for several days, causing postlarvae to remain on offshore substrates (Matthews et al., 1991). Peaks in abundance of *P. setiferus* postlarvae may be related to prior spawning activity around new or full moon phases, but this relationship is uncertain at present and warrants further investigation.

A relationship between recruitment of *P. aztecus* postlarvae and subsequent commercial landings has been difficult to demonstrate (Williams, 1969; Ford and St. Amant, 1971; Baxter and Sullivan[4]). Gener-

[4] Baxter, K. N., and L. F. Sullivan. 1986. Forecasting offshore brown shrimp catch from early life history stages. *In* Proc. shrimp yield workshop. Tex. A&M Univ. Sea Grant Rep. TAMU-SG-86-10:22–36.

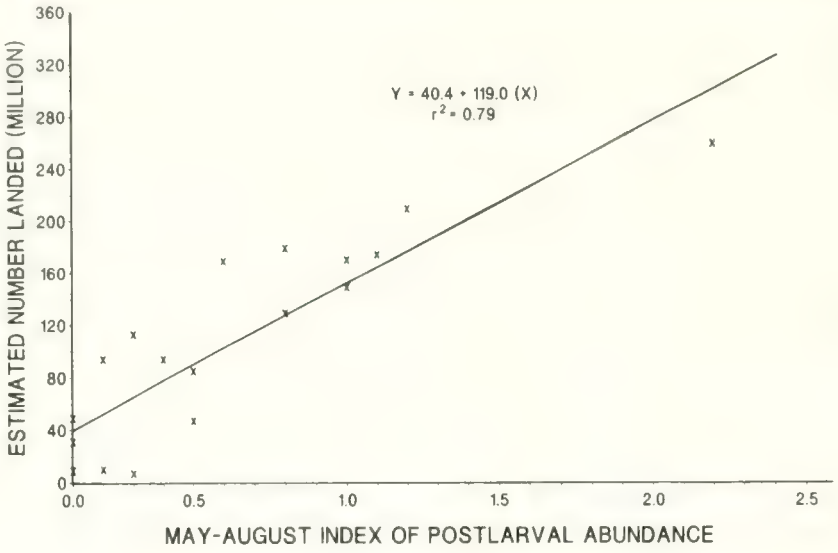

Figure 5

Plot of annual indices of abundance of postlarval white shrimp, *Penaeus setiferus*, versus estimated number of shrimp landed in the fall commercial and recreational fishery, 1975–92.

ally, environmental conditions in the nursery area, e.g. spring temperature and salinity (with related factors such as rainfall, river discharge, and meteorological conditions; Gaidry and White, 1973; Barrett and Gillespie, 1975; Zein-Elden and Renaud, 1986; Childers et al., 1990) are thought to be important influences on production. Biological factors such as predation and secondary production have also been postulated to influence yield (Hunter and Feller, 1987; Gleason and Wellington, 1988; Minello et al., 1989). Postlarval indices have been used with some success in predictive models that incorporate environmental variables and indices of juvenile shrimp abundance (Sutter and Christmas, 1983; Baxter et al., 1988). We have been unsuccessful in efforts to produce a model for brown shrimp production using data from consectutive years, although our postlarval index may be useful in the future.

Undoubtedly many factors influence the production of *P. setiferus* populations, but recent studies have demonstrated that commercial harvest of *P. setiferus* can be modeled (Lam et al., 1989) and apparent spawner-recruit relationships have been described in South Carolina (Lam et al., 1989) and in the Gulf of Mexico (Nance and Nichols, 1988; Gracia, 1991). Our study demonstrates that monitoring of *P. setiferus* postlarvae can be a reliable indicator of harvest.

Expanded sampling effort, i.e. more locations and increased numbers of samples, would perhaps yield more statistically significant results than were obtained at a single location in our study. These data do, however, represent one of the longest-term studies of postlarval penaeid recruitment to date. In addition to contributing to our overall understanding of penaeid shrimp population dynamics, our baseline monitoring effort may be useful as a management tool for predicting harvest and providing advice on optimal times for flooding coastal impoundments for extensive aquaculture.

Acknowledgments

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Literature cited

Aldrich, D. V., C. E. Wood, and K. N. Baxter.
1968. An ecological interpretation of low temperature responses in *Penaeus aztecus* and *P. setiferus* postlarvae. Bull. Mar. Sci. 18:61–71.

Allen, D. M., J. H. Hudson, and T. J. Costello.
1980. Postlarval shrimp (*Penaeus*) in the Florida Keys: species, size and seasonal abundance. Bull. Mar. Sci. 30:21–34.

Anderson, W. W.
1970. Contributions to the life histories of several penaeid shrimps (Penaeidae) along the South At-

lantic coast of the United States. U.S. Fish Wild. Serv. Spec. Sci. Rep. 605, 24 p.

Barrett, B. B., and M. C. Gillespie.
1975. 1975 environmental conditions relative to shrimp production in coastal Louisiana. La. Wild. Fish. Comm. Tech. Bull. 15, 22 p.

Baxter, K. N.
1963. Abundance of postlarval shrimp—one index of future fishing success. Proc. Gulf Caribb. Fish. Inst. 15:79–87.

Baxter, K. N., and W. C. Renfro.
1967. Seasonal occurrence and size distribution of postlarval brown and white shrimp near Galveston, Texas, with notes on species identification. Fish. Bull. 66:149–158.

Baxter, K. N., C. H. Furr Jr., and E. Scott.
1988. The commercial bait shrimp fishery in Galveston Bay, Texas, 1959–87. Mar. Fish. Rev. 50:20–28.

Bearden, C. M.
1961. Notes on postlarvae of commercial shrimp (*Penaeus*) in South Carolina. Contrib. Bears Bluff Lab. 33, 8 p.

Caillouet, C. W., Jr., B. J. Fontenot, Jr., and R. J. Dugas.
1968. Diel fluctuations in catch of postlarval white shrimp, *Penaeus setiferus* (Linnaeus), with Renfro beam trawl. Bull. Mar. Sci. 18:829–835.

Caillouet, C. W., Jr., W. S. Perret, and R. J. Dugas.
1970. Diel fluctuations in catch of postlarval brown shrimp, *Penaeus aztecus* Ives, with the Renfro beam trawl. Bull. Mar. Sci. 20:721–730.

Childers, D. L., J. W. Day, and R. A. Muller.
1990. Relating climatological forcing to coastal water levels in Louisiana estuaries and the potential importance of El Niño-southern oscillation events. Clim. Res. 1:31–42.

Christmas, J. Y., G. Gunter, and P. Musgrave.
1966. Studies of annual abundance of postlarval penaeid shrimp in the estuarine waters of Mississippi, as related to subsequent commercial catches. Gulf Res. Rep. 2:177–212.

Duronslet, M. J., J. M. Lyon, and F. Marullo.
1972. Vertical distribution of postlarval brown, *Penaeus aztecus*, and white shrimp, *Penaeus setiferus*, during immigration through a tidal pass. Trans. Am. Fish. Soc. 101:748–752.

Elliot, J. M.
1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Pub. 25, 160 p.

Ford, T. B., and L. St. Amant.
1971. Management guidelines for predicting brown shrimp, *Penaeus aztecus*, production in Louisiana. Proc. Gulf Caribb. Fish. Inst. 23:149–161.

Gaidry, W. J., III, and C. J. White.
1973. Investigations of commercially important penaeid shrimp in Louisiana estuaries. La. Wild. Fish. Comm. Tech. Bull. 8, 154 p.

George, M. J.
1962. Preliminary observations of the recruitment of postlarvae and growth of juveniles of the brown shrimp *Penaeus aztecus* Ives in Barataria Bay. La. Wild. Fish. Comm. Bien. Rep. 9:160–163.

Gleason, D. F., and G. M. Wellington.
1988. Food resources of postlarval brown shrimp (*Penaeus aztecus*) in a Texas salt marsh. Mar. Biol. 97:329–337.

Gracia, A.
1991. Spawning stock-recruitment relationships of white shrimp in the southwestern Gulf of Mexico. Trans. Am. Fish. Soc. 120:519–527.

Hunter, J., and R. J. Feller.
1987. Immunological dietary analysis of two penaeid shrimp species from a South Carolina tidal creek. J. exp. Mar. Biol. Ecol. 107:61–70.

Lam, C. F., J. D. Whitaker, and F. S. Lee.
1989. Model for white shrimp landings for the central coast of South Carolina. North Am. J. Fish. Manage. 9:12–22.

Lindner, M. J., and W. W. Anderson.
1956. Growth, migrations, spawning and size distributions of shrimp, *Penaeus setiferus*. Fish. Bull. 56:553–645.

Loesch, H.
1965. Distribution and growth of penaeid shrimp in Mobile Bay, Alabama. Publ. Inst. Mar. Sci., Univ. Tex. 10:41–58.

Matthews, T. R., W. W. Schroeder, and D. E. Stearns.
1991. Endogenous rhythm, light and salinity effects on postlarval brown shrimp *Penaeus aztecus* Ives recruitment to estuaries. J. exp. Mar. Biol. Ecol. 154:177–189.

Minello, T. J., R. J. Zimmerman, and E. X. Martinez.
1989. Mortality of young brown shrimp *Penaeus aztecus* in estuarine nurseries. Trans. Am. Fish. Soc. 118:693–708.

Nance, J. M., and S. Nichols.
1988. Stock assessments for brown, white and pink shrimp in the U.S. Gulf of Mexico, 1960–1986. NOAA Tech. Memo. SEFC-NMFS-203, 64 p.

Olmi, E. J., III.
1986. Factors affecting the abundance of penaeid shrimps in macroplankton samples from open and impounded brackish marsh systems in South Carolina. M.S. thesis, College of Charleston, Charleston, South Carolina, 95 p.

Pearson, J. C.
1939. The early life histories of some American Penaeidae, chiefly the commercial shrimp, *Penaeus setiferus* (Linn.) Fish. Bull. 49:1–73.

Ringo, R. D., and G. Zamora Jr.
1968. A penaeid postlarval character of taxonomic value. Bull. Mar. Sci. 18:471–476.

Siegel, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, 312 p.

Sutter, F. C., and J. Y. Christmas.
1983. Multilinear models for the prediction of brown

shrimp harvest in Mississippi waters. Gulf Res. Rep. 7:205–210.

Temple, R. F., and C. C. Fischer.

1967. Seasonal distribution and relative abundance of planktonic-stage shrimp (*Penaeus* spp.) in the northwestern Gulf of Mexico, 1961. Fish. Bull. 66:323–334.

Wenner, E. L., and H. R. Beatty.

1993. Utilization of shallow estuarine habitats in South Carolina, USA, by postlarval and juvenile stages of *Penaeus* spp. (Decapoda: Penaeidae). J. Crust. Biol. 13(2):280:295

Williams, A. B.

1959. Spotted and brown shrimp postlarvae (*Penaeus*) in North Carolina. Bull. Mar. Sci. 9:281–290.

1969. A ten-year study of meroplankton in North Carolina estuaries: cycles of occurrence among penaeidean shrimps. Chesapeake Sci. 10:36–47.

Williams, A. B., and E. E. Deubler.

1968. A ten-year study of meroplankton in North Carolina estuaries: assessment of environmental factors and sampling success among bothid flounders and penaeid shrimps. Chesapeake Sci. 9:27–41.

Zein-Elden, Z. P., and M. L. Renaud.

1986. Inshore environmental effects on brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, populations in coastal waters, particularly of Texas. Mar. Fish. Rev. 48 (3):9–19.

Swimbladder deflation in the Atlantic menhaden, *Brevoortia tyrannus*

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Larval clupeoid fishes usually have a pronounced cycle of swimbladder inflation and deflation (Uotani, 1973; Hunter and Sanchez, 1976; Blaxter and Hunter, 1982). Field and laboratory studies of both Atlantic (*Brevoortia tyrannus*; Hoss et al., 1989) and gulf (*Brevoortia patronus*; Hoss and Phonlor, 1984) menhaden found that larvae inflated their swimbladders during the night and deflated them during the day.

Our past studies of Atlantic menhaden larvae found that the cue for inflation is a decrease in light intensity at sunset (Hoss et al., 1989; Forward et al., 1993). Inflation occurs rapidly and begins within 5 minutes of onset of darkness. The process involves moving to the surface, swallowing air into the alimentary canal, and moving this air into the swimbladder through the pneumatic duct (Hoss et al., 1989). Menhaden have no connection (pneumatic duct) between the swimbladder and anus as do some clupeiods (Tracy, 1920). Deflation is less studied. It is hypothesized to occur by diffusion of gas from the swimbladder throughout the night and perhaps by active movement of gas to the alimentary canal and then out through the mouth and anus (Hoss and Phonlor, 1984).

The present study was undertaken to determine 1) the manner in which swimbladder deflation occurs (by diffusion or active gas movement) in Atlantic menhaden larvae, 2) the relationship between deflation and light intensity, 3) the time-course for deflation, and 4) the presence or absence of an endogenous rhythm in deflation.

Materials and methods

Atlantic menhaden, *Brevoortia tyrannus*, were spawned and reared in the laboratory (Hettler, 1983) on a 12:12 hour light-dark cycle with the dark phase beginning at 1900 hours. Lighting during the light phase was provided by daylight fluorescent tubes at a surface intensity of 1.6×10^{15} photons·cm^{-2}·s^{-1} (400–700 nm) as measured with a scalar irradiance meter with a 4π collector (Biospherical Instruments, Inc.). Our previous study found that swimbladder inflation began when larvae were 10 mm total length (TL) but the percentage with inflated swimbladders was low (Forward et al., 1993). Between 11 and 16 mm TL, swimbladders were inflated during the night and deflated during the day. Above 16 mm TL, most fish always had some gas in their swimbladders. Since the percentage of larvae with deflated swimbladders varies between day and night for 11–16 mm TL larvae, they were used in the present experiments.

Deflation was quantified by determining the proportion of larvae with deflated swimbladders. In addition, inflation was quantified by measuring the size of the light-refractive bubbles in the swimbladder and alimentary canal to the nearest 0.02 mm under a microscope. It was assumed that bubbles in the alimentary canal were transported either toward or away from the swimbladder and thereby contributed to the swimbladder volume. Gas bubble volume (v) was calculated by using the equation of Hunter and Sanchez (1976): $V=(4/3)\pi\ ab^2$, where b=half the bubble width and a=half the bubble length. Swimbladder volume was the total volume of all bubbles. Since swimbladder volume increases with larval length (Forward et al., 1993), this relationship is presented when volume is considered. Only larvae with inflated swimbladders were used to calculate the mean volume at each larval length. In contrast, the percentage of larvae with deflated swimbladders was calculated for all larvae (11–16 mm TL), because the previous study found that the proportion of larvae inflating swimbladders did not vary significantly with larval length (Forward et al., 1993).

Four sets of experiments were conducted, all of which began by removing larvae from rearing tanks and by placing them in darkness at the time of the beginning of the dark phase. Our previous study showed that darkness cued initial

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swimbladder inflation at the beginning of the night (Forward et al., 1993). In all experiments each larva was used only once. It was assumed that all test larvae could potentially inflate their swimbladders in darkness. However, the maximum percent inflation was around 92% (Fig. 1), which suggests that about 8% of the larvae were developmentally incapable of inflation. This low percentage would not alter the overall result of any experiment.

The first experiment measured swimbladder deflation in larvae kept in continuous darkness with and without access to air. Deflation was defined as the absence of gas bubbles in the swimbladder and alimentary canal. Three hours after the beginning of night (2200 hours), a subsample of the larvae was removed from the dark and measured for total length, presence of gas bubbles in the swimbladder and alimentary canal, and for size of the bubbles (standard measurements). There was no evidence that larvae lost or took up gas during the measurement procedure. The remaining larvae were separated into two groups. The first group remained in finger bowls (19.3 cm diameter) in darkness with access to the air-water interface and was similarly sampled during the following day at times (0900, 1200, and 1700 hours) that should have occurred during the normal light phase. The bowls (19.3 cm diameter) containing the second group of larvae were sealed at 2200 hours, so that larvae did not have an air-water interface. The seal was accomplished by filling the bowl completely with water and by placing a Leucite plate over the top so that no air bubbles were present. Larvae were maintained in darkness and were similarly sampled at 0900 and 1700 hours the next day.

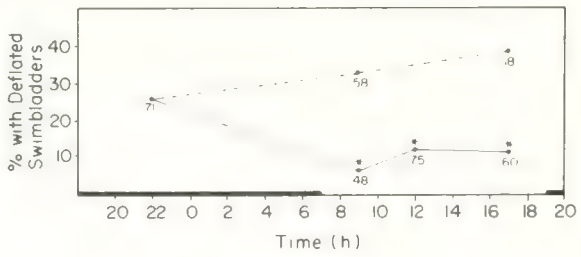

Figure 1

The percentage of larval Atlantic menhaden, *Brevoortia tyrannus*, with no gas in their swimbladder or alimentary canal (deflated) when maintained over time in continuous darkness with (solid line) and without (dashed line) access to the air-water interface. The dark bar indicates the time of the dark phase for the normal light-dark cycle. The number under each point is the sample size. An asterisk indicates the proportion with deflated swimbladders is significantly ($P<0.05$; Z-test for comparison of two proportions) different from that 3 hours after the beginning of the dark phase (initial point).

The second set of experiments was designed to determine the relationship between light intensity and swimbladder deflation. Larvae were placed in darkness at the beginning of the dark phase until two hours (0900) after the time for beginning the light phase. Larvae were then separated into two groups. For the control group standard measurements were made after three more hours of darkness. The second group was irradiated with a constant light intensity for three hours after which standard measurements were made. White light (cool white fluorescent tubes; 1.7×10^{15} photons$\cdot$cm$^{-2}\cdot$s^{-1}) was used in the initial experiment, because this was the normal daytime light during rearing. For determining the change in response with light intensity, the stimulus source was a 300-W incandescent lamp filtered to the blue region with a Corning 4-96 filter. The transmitted wavelengths encompassed the major spectral-sensitivity maxima of most fish (e.g. Munz, 1958; McFarland and Munz, 1975). All intensities below the maximum level were controlled by neutral density filters.

The third set of experiments was designed to determine the time-course for swimbladder deflation. Larvae were maintained as above in darkness until 0900 hours when standard measurements were made on control groups of larvae. The remaining larvae were then exposed to light similar to that used in the normal light phase (cool white fluorescent lamps: intensity=1.7×10^{15} photons$\cdot$cm$^{-2}\cdot$s^{-1}) and standard measurements made on subsamples at various time intervals (5, 15, 30, 60, 90, 120 min).

The fourth experiment tested for the presence of an endogenous rhythm in swimbladder deflation. A large group of larvae was removed from the rearing tank at the beginning of the dark phase and placed in darkness at a constant temperature (22°C) that was similar to the rearing temperature. Standard measurements were then made at time intervals throughout the next 28 hours on subsamples of larvae. Each subsample was placed under blue light (intensity= 4.5×10^{15} photons) for one hour, after which standard measurements were made. Differences in the effect of light on percent deflation over the 28-hour interval would suggest the presence of an endogenous rhythm.

The percentage of larvae with deflated swimbladders and the total volume of bubbles in each larva were calculated for each observation within each experiment. Means, standard deviations, and standard errors of percent data were calculated after the

data were arcsin-transformed. A Z-statistic was used to test differences between two proportions, and a Student's t-test was used to compare mean values of swimbladder volume (Walpole, 1974).

Results

To determine whether deflation was evident at the beginning of the light phase without the onset of light, percent deflation (Fig. 1) and swimbladder volume (Fig. 2) were measured in larvae kept in continuous darkness. When larvae had access to the air-water interface, there was a significant ($P<0.05$; Z-test) decrease in the percentage of fish with deflated swimbladders between three hours after beginning of the dark phase (23%) and two hours after the time for beginning of the light phase (8%). This significant decrease remained throughout the time for the light phase. In contrast, when fish had no access to the air-water interface, the percent deflation did not change significantly (Z-test) over these time intervals (Fig. 1). Thus, larvae do not sequentially inflate their swimbladders at sunset and then deflate them by gas diffusion or active processes by sunrise. Because the percentage of larvae with a deflated swimbladder decreased through the night when larvae had access to the air-water interface, larvae appear to continue to inflate their swimbladders when in darkness. Measurements of swimbladder volume (Fig. 2) support this suggestion.

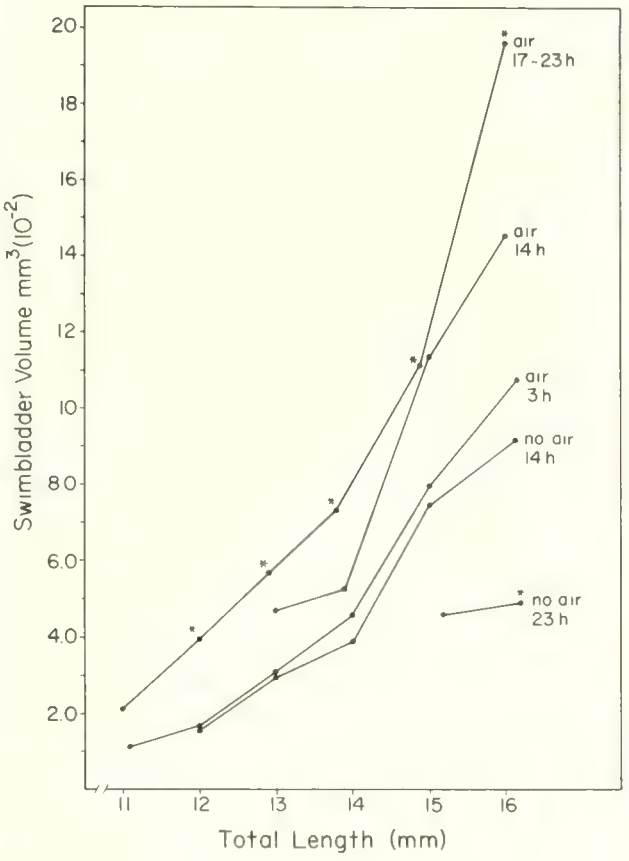

Figure 2

Swimbladder volume for different size larval Atlantic menhaden, *Brevoortia tyrannus*, with (air) and without (no air) access to the air-water interface. The times (e.g. 3 hours) indicate the time in darkness after the beginning of the dark phase when larvae were sampled. Means are plotted and the average sample sizes for calculating the means in each experiment are as follows: air for 17–23 hours=19; air for 14 hours=9; air for 3 hours=19; no air for 14 hours=7; no air for 23 hours=6. The asterisks indicate the mean volume was significantly different ($P<0.05$; Student's t-test) from the mean volume 3 hours after the beginning of the dark phase (air, 3 hours).

The swimbladder volumes over time in darkness with and without access to the air-water interface (Fig. 2) were compared to volumes after inflation at the beginning of the night phase (air, 3 hours) to indicate volume changes due to bubble ingestion and removal, and gas diffusion. Swimbladder volume increased in darkness when fish had access to the air-water interface and decreased when they lacked access. These changes were apparent after 14 hours in darkness but only become statistically significant ($P<0.05$; Student's t-test) after 17–23 hours (Fig. 2).

Thus, larvae with access to the air-water interface continued to actively inflate their swimbladder, whereas swimbladder volume slowly decreased in larvae that lacked this access. Nevertheless, shortly after the beginning of the light phase (Fig. 2; no air, 14 hours), the volumes in larvae without access to air were not significantly lower ($P>0.05$; Student's t-test) than levels after inflation at the beginning of the dark phase (air, 3 hours). Therefore, diffusion of gas from the swimbladder played a very small role in normal deflation at sunrise.

Relation of swimbladder deflation to light

Larvae deflated their swimbladders upon exposure to light. This response was demonstrated in the initial experiment, in which, at the end of the night, larvae were either maintained for three hours in darkness or exposed to white light for this time. The percentage of larvae with a deflated swimbladder in darkness was 12% ($n=75$), whereas the percentage in light was significantly ($P<0.001$; Z-test) greater at 84% ($n=25$). Further studies indicated percent deflation depended upon light inten-

sity (Fig. 3), as the percent deflation increased as light intensity increased. The lowest light intensity to evoke a significant ($P<0.05$; Z-test) increase in deflation (threshold) was 9×10^{12} photons·cm^{-2}·s^{-1}.

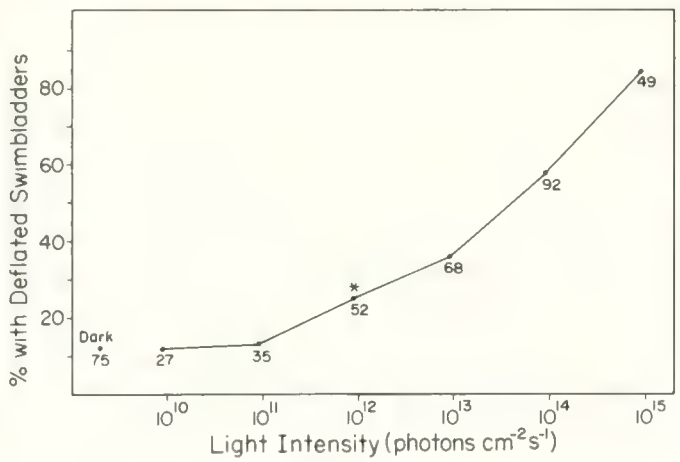

Figure 3

The percentage of larval Atlantic menhaden, *Brevoortia tyrannus*, with deflated swimbladders upon exposure to different light levels and darkness. The number below each point is the sample size. The asterisks indicate the lowest light level at which the proportion deflated was significantly ($P<0.05$; Z-test) greater than the level in darkness.

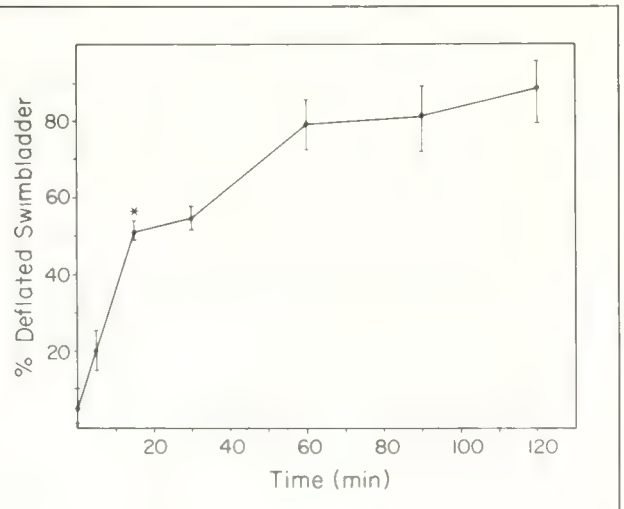

Figure 4

The percentage of larval Atlantic menhaden, *Brevoortia tyrannus*, with deflated swimbladders after different times in light. Means and standard errors are plotted. The average number of replicates was four. The asterisk indicates the first time at which the mean percent was significantly ($P<0.05$; t-test) greater than the initial level (time 0).

Timing of swimbladder deflation

The time course of swimbladder deflation in response to white light was measured upon transfer from darkness to 1.7×10^{15} photons·cm^{-2}·s^{-1}. By producing the maximum rate of light intensity change, it was assumed that the maximum rate of deflation would be evoked. An increase in the percent deflated was evident after 5 minutes and was significantly ($P<0.05$; t-test) greater than the initial level after 15 minutes (Fig. 4). Microscopic examination indicated this rapid deflation was accomplished by passing bubbles from the swimbladder into the gut and then out through both the anus and mouth.

Endogenous rhythm in swimbladder deflation

The percent deflation remained low if larvae were kept in continuous darkness (Fig. 1), which indicates there was no endogenous rhythm in deflation without exposure to light. However, light-cued deflation was not constant over time (Fig. 5). This experiment was conducted twice and involved maintaining larvae in darkness and measuring a subsample after exposure to light for one hour at different times during the solar day. The consistent cycle in both trials was that light-cued deflation was low during the normal dark phase and high during the normal day phase.

An interesting observation was made during these experiments. At the last sampling time, larvae had been in darkness for 27 hours, over which time they continued swimbladder inflation. Exposure to light at 2200 hours caused minimal deflation (Fig. 5). The water containing these larvae also had brine shrimp nauplii from the rearing tank. Larvae are visual predators and had, in effect, been starved for 27 hours in darkness. Under these conditions, once exposed to the light, they began to feed. While measuring swimbladder volumes, their digestive tracts were full of nauplii. Thus, larvae can feed with an inflated swimbladder.

Discussion

Swimbladder deflation by larval Atlantic menhaden is cued by an increase in light intensity. There was no cycle in which larvae inflated their swimbladders at sunset (Forward et al., 1993) and then deflated them gradually over time. In darkness at the end of the night, larvae, with and without air, had inflated swimbladders, and their volumes were not significantly reduced through the night. Thus, deflation

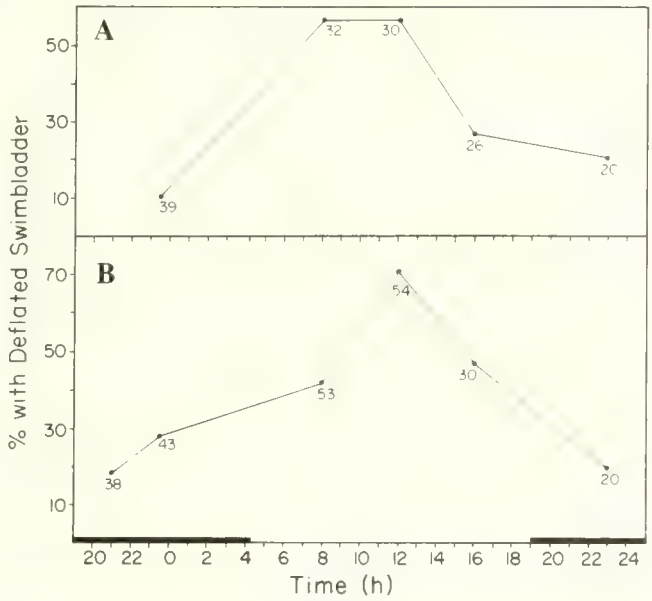

Figure 5

The percentage of larval Atlantic menhaden, *Brevoortia tyrannus*, with deflated swimbladders over the solar day. Larvae were maintained in continuous darkness and then exposed to light for one hour. The experiment was replicated twice (**A** and **B**). The dark bar indicates the time of the normal dark phase of the rearing light-dark cycle. The number under each point is the sample size.

through gas diffusion as suggested by Hoss and Phonlor (1984) did not occur.

If larvae were exposed to light near the time of the beginning of the light phase, deflation began within 5 minutes and was statistically apparent in 15 minutes. Rapid deflation occurred as the pneumatic duct opened between the gut and swimbladder and gas passed into the alimentary canal, where it was moved to both the mouth or anus for expulsion. The lowest light intensity that evoked deflation was about 10^{12} photons·cm^{-2}·s^{-1}. This threshold is below the lowest light intensity that inhibits inflation at sunset (12–16 mm larvae; 6×10^{13} photons·cm^{-2}·s^{-1}; Forward et al., 1993). Thus, larvae appear to be more sensitive to light at sunrise than at sunset. Maximum nighttime light intensity from the moon and star light is about 10^{11} photons·cm^{-2}·s^{-1} (McFarland and Munz, 1975; Lythgoe, 1979). Because this value is below the threshold intensity (10^{12} photons·cm^{-2}·s^{-1}) for deflation, moon and star light probably will not initiate deflation at night. Since surface light levels are about 10^{17} photons·cm^{-2}·s^{-1} at noon (Lythgoe, 1979), an intensity of 10^{12} photons·cm^{-2}·s^{-1} occurs earlier, probably near sunrise.

Larvae appear to have an endogenous rhythm in light-cued deflation. If they were maintained in constant darkness, light induced a low percent deflation during the night phase and a high percentage during the day phase. This rhythm is the reverse of the inflation rhythm, in which sudden darkness initiates inflation at night but rarely during the day (Forward et al., 1993). The functional significance of the deflation rhythm may be that 1) larvae do not deflate their swimbladder at night in response to any light and 2) they are "prepared" for rapid deflation at sunrise.

Field studies suggest Atlantic menhaden larvae undergo nocturnal diel vertical migration (DVM), in which they remain at moderate depths during the day and occur near the surface at night (Govoni and Pietrafesa, in press). Swimbladder inflation at sunset would increase buoyancy and reduce larval sinking rate (Hoss et al., 1989), which would maintain larvae closer to the surface. The present laboratory study supports a nocturnal DVM pattern by indicating that the percentage of larvae with inflated swimbladder and swimbladder volumes increased through the night, when larvae have access to the air-water interface. These increases are not predicted if larvae inflate their swimbladder only once at sunset and then sink. Thus, there is probably a cycle during the night, in which larvae sink while remaining motionless and then periodically return to the surface for additional gas. This pattern would retain larvae near the surface, which may be useful for transport from the offshore spawning area to the mouth of an estuary (Hoss et al., 1989).

A final consideration in the present study is why larvae deflate their swimbladders. Clearly, Atlantic menhaden larvae are adapted for deflation at sunrise. Their rhythm indicates they are most responsive to a light intensity increase at this time, and deflation occurs within 15 minutes. Such a dramatic response suggests deflation has an important functional advantage.

A fully inflated swimbladder may reduce the speed of movement and, thereby, the effectiveness of prey capture. Larvae feed during the day and use vision to find their prey (Blaxter and Hunter, 1982). Although a reduction in capture efficiency is possible, larvae with fully inflated swimbladders can still capture prey as observed in the rhythm experiment. Alternatively, an inflated swimbladder may increase detection of menhaden larvae by visual predators. Since larvae are relatively transparent, the difference in refractive index between air and water increases the contrast between an inflated swim-

bladder and the surrounding water. This increase in visibility could lead to increased predation. Thus, deflation at sunrise may be a predator avoidance response.

Acknowledgments

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Literature cited

Blaxter, J. H. S., and J. R. Hunter.
1982. The biology of clupeoid fishes. Adv. Mar. Biol. 20:1–223.

Forward, R. B., Jr., L. M. McKelvey, W. F. Hettler, and D. E. Hoss.
1993. Swimbladder inflation of the Atlantic menhaden *Brevoortia tyrannus*. Fish. Bull. 91:254–259.

Govoni, J. J., and L. J. Pietrafesa.
In press. Eulerian views of layered water currents, vertical distribution of some larval fishes and inferred advective transport over the continental shelf off North Carolina, USA, in winter. Fish. Oceanography.

Hettler, W. F.
1983. Transporting adult and larval gulf menhaden and techniques for spawning in the laboratory. Prog. Fish. Cult. 45:45–48.

Hoss, D. E., and G. Phonlor.
1984. Field and laboratory observations on diurnal swim bladder inflation-deflation in larvae of gulf menhaden, *Brevoortia patronus*. Fish. Bull. 82:513–517.

Hoss, D. E., D. M. Checklery Jr., and L. R. Settle.
1989. Diurnal buoyancy changes in larval Atlantic menhaden (*Brevoortia tyrannus*). Rap. P.-v. Reun. Cons. int. Explor. Mer. 191:105–111.

Hunter, J. R., and C. Sanchez.
1976. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull. 74:847–855.

Lythgoe, J. N.
1979. The ecology of vision. Clarendon Press, Oxford, 244 p.

McFarland, W. N., and F. W. Munz.
1975. The evolution of photopic visual pigments in fish. Vision Res. 15:1071–1080.

Munz, F. W.
1958. The photosensitive retinal pigments of fish from relatively turbid coastal waters. J. Gen. Physiol. 42:445–459.

Tracy, H. C.
1920. The membranous labyrinth and its relation to the precoelomic diverticulum of the swimbladder in clupeoids. J. Comp. Neurol. 31:219–257.

Uotani, L.
1973. Diurnal changes of gas bladder and behavior of postlarval anchovy and other related species. Bull. Jpn. Soc. Sci. Fish. 39:867–876.

Walpole, R. E.
1974. Introduction to statistics. Macmillan, New York.

An energy budget for northern sand lance, *Ammodytes dubius*, on Georges Bank, 1977–1986

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The northern sand lance, *Ammodytes dubius*, is a small planktivorous fish, classified as a "ubiquitous shelf species" (Sherman et al., 1983) and is found off the northwest Atlantic coast from North Carolina to Greenland (Nizinski et al., 1990). Sand lance are consumed by many piscivorous marine vertebrates. They have been found in the stomachs of dogfish, *Squalus* spp., skates, *Raja* spp., Atlantic cod, *Gadus morhua*, haddock, *Melanogrammus aeglefinus*, pollock, *Pollachius virens*, sculpin, *Myoxocephalus* spp., Atlantic salmon, *Salmo salar*, various flatfishes, *Paralichthys*, *Limanda*, and *Pseudopleuronectes*, and other fishes (Scott, 1968; Reay, 1970; Meyer et al., 1979; Bowman and Michaels, 1981; Winters, 1981), as well as seabirds (Backus and Bourne, 1987). Humpback whales, *Megaptera novaeangliae*, have also been observed feeding on sand lance (Payne et al., 1986). Negative correlations have been shown between the abundance of sand lance and right whales, *Eubalaena glacialis*, and it has been suggested that in the northwest Atlantic these two animals may actually compete for their primary food source, the copepod *Calanus finmarchicus* (Kenney et al., 1986; Payne et al., 1990). Therefore, although the sand lance is not commercially important, as a plankton feeder and an important prey species, it may exert significant influence over the efficiency of energy transfer from primary to higher trophic levels.

Georges Bank was chosen as a study area in which dramatic changes in the northern sand lance population might be examined in terms of the consumption and production of fish relative to the production of the region as a whole. This 41,809 km^2, 50-m deep plateau (Sherman et al., 1984) is located off the northeast coast of the United States and is a highly productive fishing ground with high annual primary production (350 g carbon$\cdot m^{-2} \cdot y^{-1}$) owing to the retention of nutrients (Sherman et al., 1984; Backus and Bourne, 1987). Because of its commercial significance, Georges Bank has been well studied. Energy budgets have been developed for the entire Bank (Cohen et al., 1982; Jones, 1984; Sissenwine et al., 1984) and offer a convenient way to examine the significance of the consumption and production of an individual species within an important area of the Northeast Shelf ecosystem.

Individual energy budgets of fish have been developed for many species (Edwards et al., 1972; Adams, 1976; Kitchell et al., 1977; Kitchell and Breck, 1980; Cho et al., 1982; Kerr, 1982; Diana, 1983; Durbin and Durbin, 1983; Rice and Cochran, 1984; Kerr and Dickie, 1985; Cui and Wooton, 1989). In this study, the energy budget of the northern sand lance was developed from experiments that measured the following parameters: growth, metabolism, feeding and assimilation efficiency (Larimer, 1992), and reproductive production. These parameters were assembled into an annual energy budget based on the daily activity of the fish in the field associated with temperature and food availability. Monthly growth was used to estimate annual ration and the budget was extrapolated to northern sand lance population abundance levels measured on Georges Bank from 1977 to 1986.[1] The potential predatory impact of the northern sand lance population on seasonal and annual zooplankton productivity on the bank[2] (Sherman et al., 1987) was examined. Finally, the annual production and consumption by these populations were compared with energy budget model values for Georges Bank.

Methods

Individual energy budget

An "average" adult northern sand lance was considered to be age 1+, the dominant age in a population of adults (Nelson, 1990). The average size was 142 mm fork length, 6.02 g wet weight, and 1.40 g dry weight based on the following wet-weight fork length relationship of Larimer (1992):

$$\text{weight} = 4.0665\ e^{-4}\ \text{length}^{3.61}.$$

The annual energy budget for an individual northern sand lance was described by the following equation adapted from Winberg (1956):

[1] Kane, J. 1992. Macrozooplankton seasonal abundances on Georges Bank, 1977–1986. NOAA, Nat. Mar. Fish. Ser., Northeast Fish. Sci. Center, Narragansett Lab., Narragansett, RI 02882. Unpubl. data.

[2] Fogarty, M. 1992. Survey biomass estimates for sand lance on Georges Bank. NOAA, Nat. Mar. Fish. Ser., Northeast Fish Sci. Center, Water Street, Wood's Hole, MA 02543. Unpubl. data.

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Fishery Bulletin 92:647–654 (1994).

$$G + R = C - M - W, \quad (1)$$

where the components (in kilocalories) are

G = somatic growth;
R = reproduction;
C = food consumption;
M = metabolism;
W = fecal loss.

Assimilated ration (A) equals consumption minus fecal losses. A small fraction of the assimilated energy is lost through nitrogenous excretion (Brett and Groves, 1979) but was not estimated in this study. The remaining portion of the assimilated energy was assumed available for growth and metabolism. The methods used to estimate each parameter are described below.

Growth

The northern sand lance growth rate is 0.87 yr^{-1} in grams, as determined by back calculation of length at age from otolith increments (Larimer, 1992). Multiplied by 6.02 g, the wet weight of an average fish, this is equivalent to a growth rate of 5.24 $g \cdot yr^{-1}$. Wet weight was converted to dry weight using the following equation (Larimer, 1992):

$$\text{dry wt.} = 0.309 \text{ wet wt.} - 0.286 \ (r^2 = 0.859).$$

The growth rate (in dry grams) was 1.20 $g \cdot fish^{-1} \cdot yr^{-1}$. Growth in kilocalories was calculated based on a mean caloric content of 6.73 kcal·dry $gram^{-1}$ (Larimer, 1992) and was 8.08 $kcal \cdot fish^{-1} \cdot yr^{-1}$.

Growth was also estimated on a monthly basis. Reay (1972) measured monthly growth in length of age 1+ *A. tobianus* off the coast of England. These fish and *A. dubius* are of similar size (range: 84–138 mm, Reay, 1972, versus 85–138 mm, Larimer, 1992) and seasonal temperatures in their habitats are similar (3–19°C off England, Reay, 1972; 3.4–14.4°C for Georges Bank, Hopkins and Garfield, 1981). Therefore, I assumed that their monthly growth rates would be similar. Reay (1972) found that *A. tobianus* grows from April to October; however, it spawns from February to March, later than the December to February spawning of *A. dubius* (Bigelow and Schroeder, 1953; Norcross et al., 1961; Reay, 1970; Colton et al., 1979; Sherman et al., 1984). Nelson and Ross (1991) found that gonadal development of *A. dubius* on Georges Bank was in progress by September. Thus, I assumed that *A. dubius* weight gain beginning in September is devoted to gonadal rather than to somatic growth, and therefore, their somatic growing season extends from April to August.

The percentage of annual growth occurring during each month of the growing season was calculated from two years of monthly growth data for *A. tobianus* as reported by Reay (1972). This monthly average was multiplied by the total annual growth measured for *A. dubius* (8.08 $kcal \cdot yr^{-1}$, see above) to determine monthly net growth in caloric content.

Reproductive energetics

Gonad weight and caloric content were measured to estimate the portion of the northern sand lance annual energy budget devoted to reproduction. In December 1990, eight fish judged to be ripe (stage III, of Macer, 1966) were measured (fork length, mm), and wet weighed (g). The gonads were extracted, weighed and dried. The dried gonads were weighed, ground to a powder with mortar and pestle, and their caloric content measured with a Phillipson microbomb calorimeter (Phillipson, 1964).

Metabolism

Metabolism was estimated for an "average" day in each month by using mean monthly water temperature calculated from averages of the top 40 m on Georges Bank (Hopkins and Garfield, 1981) and the number of hours of daylight at mid-month. I assumed the fish actively feed during half of the daylight hours. Thus, I divided a day into three periods: a nighttime resting period equivalent to the hours of darkness, a feeding period that is assumed to be half of the daylight hours, and a postfeeding period that is the remaining half of the daylight hours. Metabolic rates were estimated for each of these periods from the rates measured during similar periods at 6, 12, and 18°C (Larimer, 1992). The lowest temperature that could be maintained in the lab was 6°C so these temperatures were chosen as the best approximation of the annual temperature range on Georges Bank (Backus and Bourne, 1987). Because there was no clear relationship between metabolic rates and temperature evident in the respiration experiments (Larimer, 1992), the 6°C values were used for April, May, and December, the 12°C values were used for June, July, October, and November, and the 18°C values were used for August and September.

Assimilation efficiency

The efficiency of energy assimilation by sand lance was determined by the monthly temperature on Georges Bank (Backus and Bourne, 1987) and the relationship of assimilation efficiency to temperature found in Larimer (1992):

$$AE = 82.41 + 0.764\ T, \quad (2)$$

where AE = assimilation efficiency (%);
T = temperature (°C).

Ration estimation

Annual ration was estimated by summing the metabolic requirements, somatic growth requirements, and reproductive requirements, and then by taking assimilation efficiency into account. Because assimilation efficiency was found to increase with increasing temperature (Larimer, 1992), ration was calculated on a monthly rather than an annual basis.

Seasonal water temperatures (and therefore fish activity levels) and food availability on Georges Bank were used to estimate a monthly ration for sand lance based on the energy budget requirements. I assumed that the fish are inactive during January, February, and March. Other species of *Ammodytes* (*A. tobianus*, Reay, 1970; *A. marinus*, Macer, 1966) are known to spend the winter months buried in the sand. This behavior has not been recorded for *A. dubius* but catches of these fish during the winter months are low (Nelson, 1990) and they have been observed to spend extended periods buried in the sand in the laboratory, apparently without feeding[3] (personal observ., 1991). I assumed that the metabolic requirement for January, February, and March and the annual reproductive requirement were assimilated from May through September when food availability is high and water temperatures are still warm.

Monthly gross energy requirements were estimated by summing monthly energetic costs and multiplying by the percent of consumed calories lost as waste based on monthly assimilation efficiencies. These were divided by the caloric content of the ration (6.11 ± 0.77 kcal·g^{-1} for *Calanus finmarchicus*; Larimer, 1992) to determine the actual grams of ration required per month. The sum of these monthly estimates is the yearly ration requirement.

Population energy budget

The energy budget for individual adult northern sand lance was extrapolated to the population level by multiplying overall production (growth+reproduction) and consumption (predicted ration) by the number of individuals estimated to be present on Georges Bank from 1977 through 1986. Northern sand lance population size was estimated from spring sand lance biomass estimates for 1977–86.[2] Mean sand lance weight per tow was divided by mean individual adult fish wet weight (see above) and the average tow volume to estimate the number of individuals present per unit volume on the Bank. There were no sand lance abundance data for 1979. The energy budget parameters of the population were then compared with estimates of secondary production on Georges Bank.

Macrozooplankton production (including *Calanus finmarchicus*, *Pseudocalanus minutus*, *Centropages* species, and *Metridia lucens*) on Georges Bank was calculated from population estimates measured during the MARMAP surveys from 1977 to 1986 (Sherman et al., 1987). Zooplankton volumes were reported in Kane.[1] These were transformed into annual production values following Sherman et al. (1987) where volume is converted to biomass using the following equation (Wiebe et al., 1975):

$$\log_{10}(\text{dry weight}) = \log_{10}(\text{volume} + 1.828)/0.848.$$

A value of 5.25 kcal·g^{-1} (Laurence, 1976) and a production-to-biomass ratio (P:B) of 7 (Steele, 1974; Crisp, 1975) were used to convert zooplankton biomass to production. Annual production was estimated for each year of available zooplankton data (1977–86) and compared with the calculated annual consumption by northern sand lance.

Results and discussion

Predicted ration and individual budget

The ratio of production to consumption (P:C) determined from an individual energy budget represents the gross ecological growth efficiency of an animal within a trophic level (Slobodkin, 1960). This ratio was determined from the individual energy budget for the northern sand lance. Monthly growth estimates calculated from Reay's (1972) data range from 0% from September to March to 36% dry body weight in May (Table 1) and from 0.00 kcal, from Septem-

Table 1

Monthly somatic growth of northern sand lance, *Ammodytes dubius*, on Georges Bank estimated from measurements of *A. tobianus* growth rates in length (Reay, 1972) and the availability of food on the Bank. Reay measured no net growth September through March.

Month	% Growth (wt)	Growth (kcal)
April	0.14	1.15
May	0.36	2.90
June	0.19	1.50
July	0.07	0.56
August	0.24	1.97

[3] Halavik, T. NOAA, Nat. Mar. Fish. Ser., Northeast Fish. Sci. Center, Narragansett Lab, Narragansett, R.I. 02882. Personal commun., September 1991.

Table 2

Monthly energy requirements for northern sand lance, *Ammodytes dubius*, on Georges Bank. Fish are assumed to be inactive in January, February, and March; therefore metabolic energy requirements for those months ("nonfeed metabolism"), as well as annual reproductive energy requirements, were divided equally over the months of highest temperature and food availability.

Month	Metabolic cost (kcal)	Somatic growth (kcal)	Reproductive growth (kcal)	Nonfeed metabolism (kcal)	Energy required (kcal)
January	2.23	0.00	0.00	0.00	0.00
February	2.02	0.00	0.00	0.00	0.00
March	2.23	0.00	0.00	0.00	0.00
April	3.90	1.15	0.00	0.00	5.05
May	4.15	2.90	0.49	1.29	8.83
June	3.33	1.50	0.49	1.30	6.62
July	3.38	0.56	0.49	1.30	5.73
August	3.57	1.97	0.49	1.30	7.33
September	3.33	0.00	0.49	1.29	5.11
October	3.07	0.00	0.00	0.00	3.07
November	2.91	0.00	0.00	0.00	2.91
December	3.44	0.00	0.00	0.00	3.44

Table 3

Gonad weight and energy content of northern sand lance, *Ammodytes dubius*, from Georges Bank.

	Males	Females	Total mean
N	1	7	8
Fork length (mm)	132	127±7.4	128±7.1
Dry weight (g)	1.23	1.22±0.35	1.23±4.94
Gonad (% dry body weight)	14.33	26.36±2.72	24.85±4.94
Gonad (kcal/g)	6.4	7.12±0.52	7.03±0.54

Table 4

Calculated monthly respiration requirements in kilocalories for northern sand lance, *Ammodytes dubius*, on Georges Bank. Fish are assumed to be inactive from January to March.

Month	°C	Hours of light	Kcal used per month
January	6.1	9.5	2.23
February	4.3	10.5	2.02
March	3.4	12.0	2.23
April	3.4	13.5	3.90
May	7.7	14.5	4.15
June	10.9	15.5	3.33
July	13.0	15.0	3.38
August	14.4	14.0	3.57
September	14.3	12.5	3.33
October	13.2	11.0	3.07
November	11.0	10.0	2.91
December	8.8	9.0	3.44
Annual total			37.56

ber to March, to 2.90 kcal in May (Table 2). The mean percent of body weight accounted for by the ripe gonads, 24.85%, is similar to the 20–30% measured for age 1+ *A. personatus* (Okamoto et al., 1989) and the 25–28% measured for both male and female *A. americanus* (Smigielski et al., 1984), (Table 3). Estimated monthly metabolic requirements range from a low in February of 2.03 kcal to a high in May of 4.15 kcal (Table 4). The annual individual energy requirement was 37.56 kcal (Table 4). Monthly assimilation efficiencies and daily rations are shown in Table 5, and the predicted annual ration is 52.62 kcal·fish^{-1} or 8.60 g·fish^{-1} (assuming a caloric content of 6.11 kcal·g^{-1} for *C. finmarchicus*; Larimer, 1992). The energy assimilated from that ingested is 48.09 kcal·fish^{-1} so the annual individual energy budget in terms of kilocalories is approximated by

$$(G) + (R) = (AR) - (R), \qquad (3)$$

where growth (G) = 8.08 kcal·yr^{-1};
reproduction (R) = 2.45 kcal·yr^{-1};
assimilated ration (AR) = 48.09 kcal·yr^{-1};
respiration (R) = 37.56 kcal·yr^{-1}.

If the budget is converted into percentage of total consumption accounted for by each parameter, the following relationship results:

Table 5

Predicted daily ration of adult northern sand lance, *Ammodytes dubius*, on Georges Bank based on monthly growth (Table 1) and assimilation efficiency for *Calanus finmarchicus* (Equation 2).

Month	Assimilation efficiency (%)	Required energy (kcal/month)	Ration (kcal/month)	Ration (g/month)	Daily ration (% body wt)
January	87.07	0.00	0.00	0.00	0.00
February	85.70	0.00	0.00	0.00	0.00
March	85.01	0.00	0.00	0.00	0.00
April	85.01	5.05	5.81	0.95	2.26
May	88.29	8.83	9.86	1.61	3.72
June	90.74	6.62	7.23	1.18	2.82
July	92.34	5.73	6.17	1.01	2.33
August	93.41	7.33	7.81	1.28	2.95
September	93.34	5.11	5.45	0.89	2.12
October	92.49	3.07	3.30	0.54	1.24
November	90.81	2.91	3.18	0.52	1.24
December	89.13	3.44	3.81	0.62	1.44
Annually		48.09	52.62	8.60	

Table 6

Annual consumption of adult northern sand lance, *Ammodytes dubius*, on Georges Bank, based on individual energy budget requirements extrapolated to population levels from 1977 through 1986. These values are compared to average annual zooplankton productivity for each year. The percent of production consumed by sand lance is shown for each year.

Year	Sand land abundance (no. per m^3)	Annual consumption ($kcal/m^3/yr$)	Zooplankton production ($kcal/m^3/yr$)	% consumed by sand lance
1977	0.0198	1.03	45.56	2.27
1978	0.0261	1.63	32.07	5.08
1980	0.0782	4.07	21.16	19.24
1981	0.0143	0.74	22.89	3.24
1982	0.0261	1.36	16.25	8.37
1983	0.0091	0.48	12.77	3.76
1984	0.0056	0.29	14.56	1.99
1985	0.0032	0.17	21.58	0.79
1986	0.0081	0.42	18.49	2.27

$$100C = 15G + 5R + 71M + 9W, \quad (4)$$

where C = consumption;
G = growth;
R = reproduction;
M = metabolic requirement;
W = waste (that portion of the predicted ration that is not assimilated based on Equation 2 above).

For an individual adult northern sand lance on Georges Bank, total production is 10.53 $kcal \cdot yr^{-1}$ (growth+reproduction), and total consumption is 52.62 $kcal \cdot yr^{-1}$(Table 5); therefore, ecological efficiency is 20.0%.

Population energy budget

Northern sand lance consumed a significant proportion of total annual zooplankton production of Georges Bank from 1977 through 1986. Population abundance of northern sand lance from 1977 through 1986 was negatively correlated with zooplankton abundances during the same period (r^2=0.683, P<0.05; Fig. 1). Northern sand lance consumed 0.79–19.24% of the annual zooplankton production from 1977 to 1986 (Table 6; Fig. 2).

The trophic efficiency of the northern sand lance is 20%, according to the present energy budget model. Jones's (1984) Georges Bank energy model found that

the primary productivity of the Bank adequately accounted for fish production only if a trophic transfer efficiency of greater than 10% was assumed. This may be a valid assumption for the model at the trophic level of the northern sand lance.

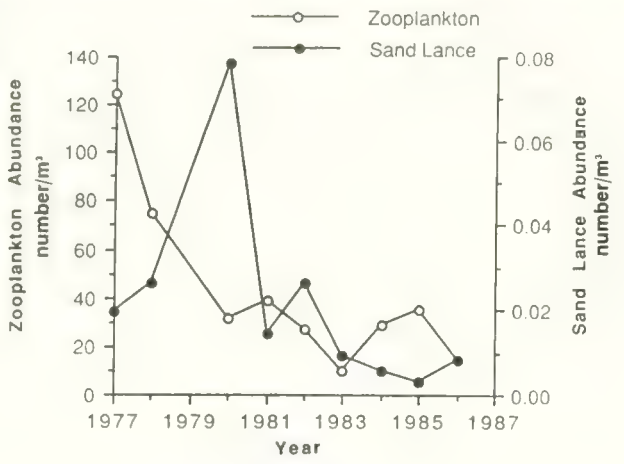

Figure 1

Average annual copepod abundance of *Calanus finmarchicus*, *Pseudocalanus minutus*, *Centropages hamatus*, *C. typicus*, *Metridia lucens*, and of adult northern sand lance, *Ammodytes dubius*, on Georges Bank from 1977 through 1986.

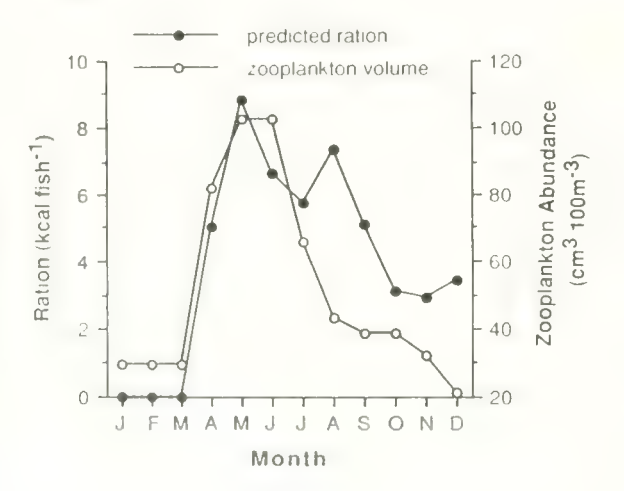

Figure 2

Mean monthly zooplankton biomass of *Calanus finmarchicus*, *Pseudocalanus* species, *Paracalanus parvus*, and *Centropages* species on Georges Bank (Sherman et al., 1987) and monthly ration required for an individual adult northern sand lance, *Ammodytes dubius*, based on the individual energy budget.

In their budget of Georges Bank bioenergetics, Sissenwine et al. (1984) place sand lance in their "other finfish" compartment (all nonfished species that are vulnerable to fishing gear). From 1973 to 1975 a consumption of 9.3 kcal·m^{-2}·y^{-1} was attributed to this category. Sissenwine et al. (1984) suggested that the impact of the sand lance population was underestimated in their budget, and it appears from the present study, based on the individual energy budget and population size, that this error was potentially significant. By converting population energetic consumption on Georges Bank (Table 6) to consumption per square meter (assuming a mean depth on the Bank of 50 m; Backus and Bourne, 1987), sand lance consumed from 8.5 to 203.5 kcal·m^{-2}·y^{-1} from 1977 to 1986. This represents nearly all the consumption attributed to the "other finfish" at low northern sand lance abundances and over 20 times the total "other finfish" consumption at high northern sand lance abundances. The results of this study suggest that the budget estimates of annual consumption by exploitable but commercially undesirable fishes may need to be revised upward.

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Literature cited

Adams, S. M.
1976. The ecology of eelgrass, *Zostera marina* (L.), fish communities. II: Functional analysis. J. exp. Mar. Biol. Ecol. 22:293–311.

Backus, R. H., and D. W. Bourne (eds.).
1987. Georges Bank. M.I.T. Press, Cambridge, MA, 593 p.

Bigelow, H. B., and W. C. Schroeder.
1953. Fishes of the Gulf of Maine. Fish. Bull. Fish and Wildl. Ser. 53, 577 p.

Bowman, R. E., and W. Michaels.
1981. Food habits of seventeen species of northwest Atlantic fish. NOAA Tech. Memo. NMFS-F/NEC-28.

Brett, J. R., and T. D. D. Groves.
1979. Physiological energetics. *In* W. S. Hoar, D. J. Randall, and J. R. Brett (eds.), Fish physiology, Vol. 8. Academic Press, 786 p.

Cho, C. Y., S. J. Slinger, and H. S. Bayley.
1982. Bioenergetics of salmonid fishes: energy, intake, expenditure, and productivity. Comp. Biochem. Physiol. 73B:25–41.

Cohen, E. B., M. D. Grosslein, M. P. Sissenwine, F. Steimle, and W. R. Wright.
1982. An energy budget for Georges Bank. Can. Spec. Publ. Fish. Aquat. Sci. 59:95–107.

Crisp, D. J.
1975. Secondary productivity in the sea. *In* D. F. Reichle, J. F. Franklin, and D. W. Goodal (eds.), Productivity of world ecosystems, p. 71–90. Washington, D.C., National Academy of Sciences.

Cui, Y., and R. J. Wooton.
1989. Bioenergetics of growth of a cyprinid *Phoxinus phoxinus* (L.): development and testing of a growth model. J. Fish Biol. 34:47–64.

Diana, J. S.
1983. An energy budget for northern pike (*Esox lucius*). Can. J. Zool. 61:1968–1975.

Durbin, E. G., and A. G. Durbin.
1983. Energy and nitrogen budgets for the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae), a filter feeding planktivore. Fish. Bull. 81:177–199.

Edwards, R. R. C., D. M. Finlayson, and J. H. Steele.
1972. An experimental study of oxygen consumption, growth, and metabolism of the cod (*Gadus morhua* L.). J. exp. Mar. Biol. Ecol. 8:299–309.

Hopkins, T. S., and N. Garfield III.
1981. Physical origins of Georges Bank water. J. Mar. Res. 39:465–500.

Jones, R.
1984. Some observations on energy transfer through the North Sea and Georges Bank food webs. Rapp. P.-v. Reun. Cons. int. Explor. Mer 183:204–217.

Kenney, R. D., M. A. M. Hyman, R. E. Owen, G. P. Scott, and H. E. Winn.
1986. Estimation of prey densities required by western North Atlantic right whales. Mar. Mammal Sci. 2:1–13.

Kerr, S. R.
1982. Estimating the energy budgets of actively predatory fishes. Can. J. Fish. Aquat. Sci. 39:371–379.

Kerr, S. R., and L. M. Dickie.
1985. Bioenergetics of 0+ Atlantic herring (*Clupea harengus harengus*). Can. J. Fish. Aquat. Sci. 42:105–110.

Kitchell, J. F., and J. E. Breck.
1980. Bioenergetics model and foraging hypothesis for sea lamprey (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 37:2159–2168.

Kitchell, J. F., D. J. Stewart, and D. Weininger.
1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34:1922–1935.

Larimer, S.
1992. Aspects of the bioenergetics and ecology of sand lance of Georges Bank. Ph.D. diss., Univ. Rhode Island, 300 p.

Laurence, G. C.
1976. Caloric values of some north Atlantic calanoid copepods. Fish. Bull. 741:218–220.

Macer, C. T.
1966. Sand eels (Ammodytidae) in the south-western North Sea; their biology and fishery. Fish. Invest. Lond. Ser. 2, 24:1–55.

Meyer, T. L., R. A. Cooper, and R. W. Langton.
1979. Relative abundance and food habits of the American sand lance, *Ammodytes americanus*, from the Gulf of Maine. Fish. Bull. 77:243–253.

Nelson, G. A.
1990. Population biology and dynamics of northern sand lance (*Ammodytes dubius*) from the Gulf of Maine to the Middle Atlantic Bight region. M.S. thesis, Univ. Mass., 202 p.

Nelson, G. A., and M. R. Ross.
1991. Biology and population changes of northern sand lance (*Ammodytes dubius*) from the Gulf of Maine to the Middle Atlantic Bight. J. Northwest Atl. Fish. Sci. 11:11–27.

Nizinski, M. S., B. B. Collette, and B. B. Washington.
1990. Separation of two species of sand lances, *Ammodytes americanus* and *A. dubius*, in the western North Atlantic. Fish. Bull. 88:241–255.

Norcross, J. J., W. H. Massmann, and E. B. Joseph.
1961. Investigations on Investigations on inner continental shelf waters off lower Chesapeake Bay. Part II: Sand lance larvae, *Ammodytes americanus*. Chesapeake Sci. 2:49–59.

Okamoto, H., H. Sato, and K. Shimazi.
1989. Comparison of reproductive cycle between two genetically distinctive groups of sand lance (genus *Ammodytes*) from northern Hokkaido. Nippon Suisan Gakkaishi 55:1935–1940.

Payne, P. M., J. R. Nicolas, L. O'Brien, and K. D. Powers.
1986. The distribution of the humpback whale *Megaptera novaeangliae* on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel *Ammodytes americanus*. Fish. Bull. 84:271–277.

Payne, P. M., D. N. Wiley, S. B. Young, S. Pittman, P. J. Clapham, and J. W. Jossi.
1990. Recent fluctuations in the abundance of baleen whales in the southern Gulf of Maine in relation to changes in selected prey. Fish. Bull. 88:687–696.

Phillipson, J.
1964. A miniature bomb calorimeter for small biological samples. Oikos 15:130–139.

Reay, P. J.
1970. Synopsis of biological data on North Atlantic sand eels of the genus *Ammodytes*. F.A.O. Fisheries Synopsis 82, 71 p.
1972. The seasonal pattern of otolith growth and its application to back-calculation studies in

Ammodytes tobianus L. J. Cons. int. Explor. Mer 34:485–504.

Rice, J. A., and P. A. Cochran.
1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology 65:732–739.

Scott, J. S.
1968. Morphometrics, distribution, growth, and maturity of offshore sand lance (*Ammodytes dubius*) on the Nova Scotia banks. J. Fish. Res. Board Can. 25:1775–1785.

Sherman, K., R. Lasker, W. Richards, and A. W. Kendall Jr.
1983. Ichthyoplankton and fish recruitment studies in large marine ecosystems. Mar. Fish. Rev. 45:1–25.

Sherman, K., W. Smith, W. Morse, M. Berman, J. Green, and L. Ejsymont.
1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Serv. 18:1–19.

Sherman, K., W. G. Smith, J. R. Green, E. B. Cohen, M. S. Berman, K. A. Marti, and J. R. Goulet.
1987. Zooplankton production and the fisheries of the northeastern shelf. *In* R. H. Backus and D. W. Bourne (eds.), Georges Bank, p. 268–282. M.I.T. Press, Cambridge, MA.

Sissenwine, M. P., E. B. Cohen, and M. D. Grosslein.
1984. Structure of the Georges Bank ecosystem. Rapp. P.-v. Reun. Cons. int. Explor. Mer 183:243–254.

Slobodkin, L. B.
1960. Ecological energy relationships at the population level. Am. Nat. 94:213–236.

Smigielski, A. S., T. A. Halavik, L. J. Buckley, S. M. Drew, and G. C. Laurence.
1984. Spawning, embryo development, and growth of the American sand lance *Ammodytes americanus* in the laboratory. Mar. Ecol. Prog. Ser. 14:287–292.

Steele, J. H.
1974. The structures of marine ecosystems. Harvard Univ. Press, Cambridge, MA, 128 p.

Wiebe, P. H., S. Boyd, and J. L. Cox.
1975. Relationships between zooplankton displacement volume, wet weight, dry weight, and carbon. Fish. Bull. 73:777–786.

Winberg, G. G.
1956. Rate of metabolism and food requirements of fishes. Belorussian State Univ., Minsk. Fish. Res. Board Can. Transl. Ser. 194, p. 1–256.

Winters, G. H.
1981. Growth patterns in sand lance, *Ammodytes dubius*, from the Grand Bank. Can. J. Fish. Aquat. Sci. 38:841–846.

Movements of tagged adult yellowtail rockfish, *Sebastes flavidus*, off the west coast of North America

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The Department of Fisheries and Oceans, Canada, and the University of Alaska conducted independent tagging studies on yellowtail rockfish, *Sebastes flavidus*, in the early 1980's. The Canadian study was designed to validate ageing methodology for rockfishes (Leaman and Nagtegaal, 1987). The Alaskan study was part of a larger survey of nearshore bottomfish resources in southeastern Alaska.[1,2] While neither study was designed to quantify the extent of this species' movement, the recoveries provided new insight into rockfish behavior and new implications for the management of this species.

Tagging studies of shallow demersal (<100 m) species of rockfish, *Sebastes* spp., have typically indicated very limited movement (Table 1), with the exception of a report of a brown rockfish, *S. auriculatus*, that travelled over 50 km from San Francisco Bay.[3] Authors have also suggested limited movement for the deeper demersal or "slope" rockfish species, such as Pacific ocean perch, *S. alutus*, that are found along the continental slope at depths greater than 200 m (Fadeev, 1968; Gunderson, 1971; Wishard et al., 1980; Leaman and Kabata, 1987). While they appear to make seasonal bathymetric migrations, the available evidence from commercial fishing patterns, parasite occurrence, and age/size compositions have led investigators to hypothesize that these species make very limited latitudinal movements along the continental shelf. However, because of decompression and other injuries associated with surfacing from depths of over 200 m, no tagging studies have been performed to test this hypothesis.

It is the semi-pelagic species that inhabit the continental shelf (100–200 m) which appear to exhibit significant movement. Studies of black rockfish, *S. melanops*, and immature yellowtail rockfish indicate that at least some individuals move long distances. In northern Puget Sound (Fig. 1), Mathews and Barker (1983) tagged 123 black and 153 yellowtail rockfish. Three of eight black rockfish and eight of 10 confirmed yellowtail rockfish recoveries came from the west coast of Washington at distances up to 400 km from the release site. Because the yellowtail rockfish were all immature, the authors proposed an ontogenetic movement offshore in conjunction with reproductive maturation. Similarly, Barss[4] reported that 12 of 23 recovered immature canary rockfish, *S. pinniger*, travelled more than 100 km along the Oregon coast. Culver (1987) provided the first evidence of long distance movement of adult or reproductively mature rockfish. He recovered 484 tags from 14,795 black rockfish tagged off Washington and northern Oregon. One fish, which had been tagged off Oregon, was recovered off northern California, 555 km south of its release site. More than 12% of the recovered black rockfish moved farther than 80 km.

Contrary to those reports, which documented long distance move-

[1] Rosenthal, R. J., L. J. Field, and D. Meyer. 1981. Survey of nearshore bottomfish in the outside waters of southeastern Alaska. Alaska Coastal Research, P. O. Box 368, Langley WA, 98260. Final report to State of Alaska, Dep. Fish Game, Comm. Fish. Div. Juneau, 84 p.

[2] Rosenthal, R. J., L. Haldorson, L. J. Field, and V. M. O'Connell. 1982. Inshore and shallow offshore bottomfish resources in the southeastern Gulf of Alaska. Alaska Coastal Research, P. O. Box 368, Langley WA, 98260. Final report to State of Alaska, Dep. Fish Game, Comm. Fish. Div. Juneau, 166 p.

[3] Lenarz, W. Tiburon Laboratory, Nat. Mar. Fish. Serv., CA 94920. Personal commun., March 1993.

[4] Barss, B. Marine Science Center, Oregon Dept. Fish. Wildl., Newport, OR 97365. Personal commun., December 1985.

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ment, studies of blue rockfish, *S. mystinus* (Miller and Geibel, 1973) and olive rockfish, *S. serranoides* (Love, 1980), as well as other studies of yellowtail rockfish (Carlson and Haight, 1972; Pearcy, 1992), indicate much more limited movement. In fact, dispersal from the tagging site was so limited in the latter two studies that the authors hypothesized that yellowtail rockfish have strong homing tendencies and exhibit site fidelity. However, these two studies were conducted over limited spatial and temporal scales.

The purpose of this note is to examine the hypothesis of limited versus extensive movement of yellowtail rockfish. We use data from our two studies, which cover a broader time and space coverage than those studies that implied limited movement. We present the details of the 42 recaptures, discuss some of the factors which may have influenced the overall likelihood of recapture, and conclude with a comment on the management implications of the results.

Table 1

Reports of rockfish, *Sebastes spp.*, movement.

Species	No. of recoveries	Max. dist. moved, (km)	Literature cited
Demersal species			
Black-and-yellow rockfish,			
S. chrysomelas	38	<1	Larson, 1980
Brown rockfish,			
S. auriculatus	22[1]	<1	Matthews et al., 1987
	16	<2	Hartmann, 1987
	1	>50	Lenarz, footnote 3 in text
	11	<2	Gowan, 1983
China rockfish,			
S. nebulosus	13	<1	McElderry, 1979
Copper rockfish,			
S. caurinus	[2]	[2]	Gascon and Miller, 1981
	11[1]	<1	Mathews and Barker, 1983
	29	<1	Matthews et al., 1987
	16	<3	Hartmann, 1987
	75	<3	Gowan, 1983
Gopher rockfish,			
S. carnatus	49	<1	Larson, 1980
Quillback rockfish,			
S. maliger	12	<3	Mathews and Barker, 1983
	28[1]	<1	Matthews et al., 1987
Yelloweye rockfish,			
S. ruberrimus	7	<1	Coombs, 1979
	3	<1	O'Connell, 1991
Semi-pelagic species			
Black rockfish,			
S. melanops	61	<1	McElderry, 1979
	40	<50	Gowan, 1983
	8	400	Mathews and Barker, 1983
	484	555	Culver, 1987
	9	619	Coombs, 1979
Blue rockfish,			
S. mystinus	168	24	Miller and Geibel, 1973
	98	43	Hartmann, 1987
Bocaccio			
S. paucispinis	66	148	Hartmann, 1987
Olive rockfish,			
S. serranoides	435	<33	Hartmann, 1987
Vermilion rockfish,			
S. miniatus	1	10	Turner et al., 1969
Yellowtail rockfish,			
S. flavidus	76	<23	Carlson and Haight, 1972
	10	144	Mathews and Barker, 1983
	25	<4	Pearcy, 1992

[1] Repeated dive observations of tagged fish.
[2] Tagged fish showed strong site fidelity, no numbers provided.

Methods

Methodology used in the Canadian program, which was conducted from 1980 to 1982, has been described in detail (Shaw et al., 1981). The primary area of tagging was off southwest Vancouver Island; additional tagging was performed in Queen Charlotte Sound (Figs. 2 and 3). Fish were captured by trawl at depths of 70–80 m over bottom depths of 110–130 m. Prior to tagging, all fish were anaesthetized with tricaine methanesulphonate (MS-222). Fish with hyperinflated swim bladders were deflated with a hypodermic needle to remove excess gas (Gotshall, 1964), measured to the nearest cm (fork length), and tagged with an external Floy anchor tag imbedded in the dorsal musculature between the pterygiophores. Most fish were injected with oxytetracycline (OTC) (50 mg/kg body wt.) (Leaman and Nagtegaal, 1987). All fish were held for one hour in covered tanks with a continuous flow of seawater. Fish from the last haul of each day were held overnight. Condition after tagging and after release was assessed by using a numerical index based on several categories of injuries (Shaw et al., 1981). We did not record sex of released specimens but did examine

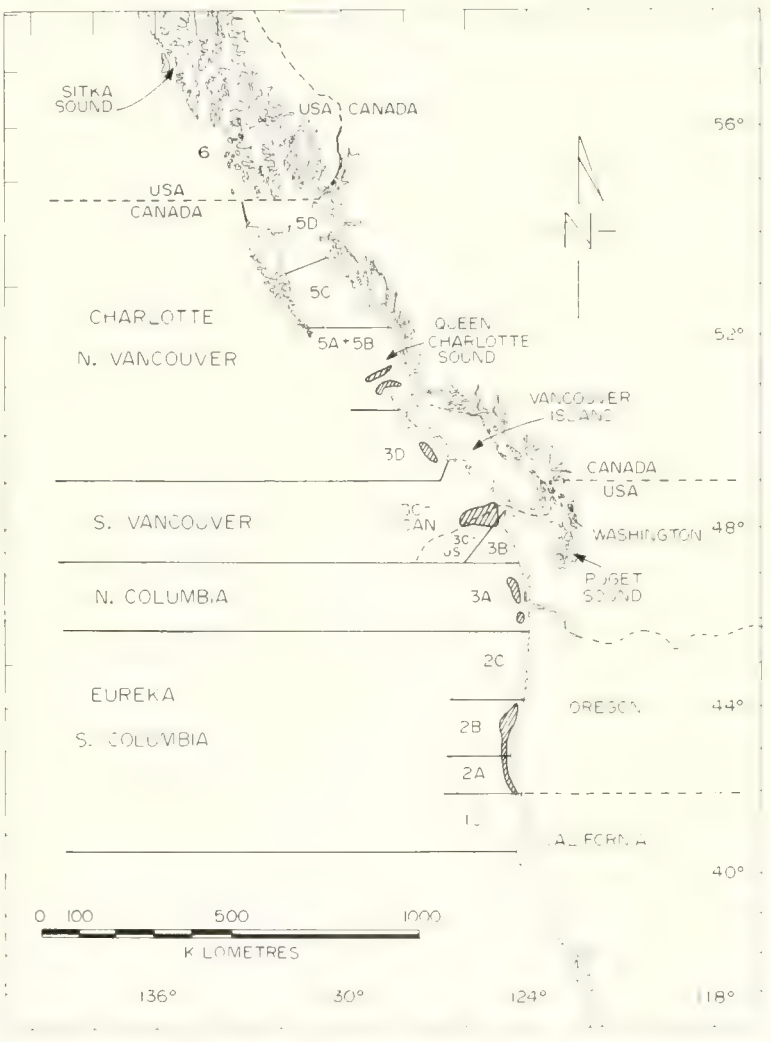

Figure 1

Sites of major yellowtail rockfish, *Sebastes flavidus*, fishing grounds (hatched areas); stock designations are based on individual or combinations of International North Pacific Fishery Commission (INPFC) statistical areas (ie. N. Columbia) and Pacific States Marine Fishery Commission (PSMFC) statistical boundaries within the INPFC areas (ie. 3C-US).

two samples of 100 fish sacrificed during the 1980 tagging off the southwest coast of Vancouver Island.

In the Alaskan program of 1981 and 1982, fish were caught by hook and line from depths of 40–100 m with commercial jigging machines. Fish were examined for decompression stress and hooking damage. Only those fish with no visible stress symptoms were tagged. A total of 397 yellowtail rockfish were tagged as in the Canadian study, but none was injected with OTC or decompressed. All fish were captured and released in July 1982 at two sites in Sitka Sound, Alaska (Fig. 2).

All tag recoveries from both programs were obtained from commercial fisheries. Data on gender and recovery location were obtained when possible, although the latter information was usually limited to statistical area. We calculated the minimum possible distance travelled by assuming the fish travelled a direct course approximating the edge of the continental shelf. Distance was calculated to the border of the statistical area closest to the point of release and rounded down to the nearest 25-km interval. Transit time was calculated as the overall distance divided by the number of days at large. The recovery

ratios (number recovered divided by number released) for the two studies were compared with a two-tailed test of binomial proportions (Kalbfleisch, 1976). We used maturity ogives from Tagart (1991) to infer the proportion mature for specific lengths. He reported 50% maturity at 39.6 cm and 45.4 cm for males and females, respectively, for fish from northern Washington.

We conducted a linear regression of the natural log of number recovered against time (0.5 years–9.5 years) for the Canadian releases to derive a point estimate of the instantaneous annual rate of extinction.

Figure 2

Number of releases (in hatched areas) and recoveries (in circles) of yellowtail rockfish, *Sebastes flavidus*, tagged in southeast Alaska and Queen Charlotte Sound.

Results

Canadian-tagged fish

The Canadian program tagged and released 4,895 fish off central British Columbia (B.C.) and 9,557 off southern B.C. and northern Washington waters. Thirty-seven have been recovered, all from commercial catches from Oregon, Washington, and B.C. waters (Figs. 2 and 3; Table 2). Of these, 36 were accompanied by reliable information on recapture location. Twenty-seven of the 36 (75%), moved less than or equal to 25 km from the release location. However, among the nine fish that travelled more than 25 km, three moved at least 100 km, three others at least 125 km, and one at least 250 km. The farthest displacements of Canadian-tagged fish were one fish that moved from Queen Charlotte Sound to the southwest coast of Vancouver Island (400 km) and one that moved from southwest Vancouver Island to southern Oregon (400 km). The most rapid movements from original tagging sites were two recoveries of Canadian-tagged fish that moved from the north coast of Washington to northern Oregon. One travelled at least 100 km in 73 days (1.37 km/day) whereas the other travelled at least 125 km in 100 days (1.25 km/day).

Average fork length of Canadian-tagged fish was 44.5 cm (23–58 cm). Recovered specimens averaged 45.9 cm (33–54 cm). Among the 21 recoveries for which sex was known, only two were probably immature at the time of release, based on their sex and lengths. Among the nine individuals that travelled further than 25 km, we know the sex of seven. Of these, only one, a 33-cm male, was likely to have been immature at the time of release.

The rate of recoveries from the Canadian study gradually declined over time (Table 3). The point estimate of the instantaneous annual rate of extinction was 0.2. However, the 95% confidence range (0.099–0.307) was wide, reflecting the low number of recoveries.

Alaskan-tagged fish

Of the 397 yellowtail rockfish tagged in Alaska, five have been recovered. All five travelled south to B.C. or to Washington waters over distances of 425–1400 km. The fish were tagged in 1982 but were not recovered until at least 1987. Time at liberty ranged from 1,827 to 2,842 days. The opportunity for recovery of yellowtail rockfish in southeastern Alaska commercial fisheries was limited. The total reported commercial catch in 1991 was three tons; the sport catch was negligible.[5] However, the recovery ratio of Alas-

[5] O'Connell, V. Alaska Dept. Fish Game, Sitka, AK 99835. Personal commun., February 1991.

Table 2

Recoveries of tagged yellowtail rockfish, *Sebastes flavidus*, by the Department of Fisheries and Oceans, Canada, and the University of Alaska; Figure 1 indicates Pacific States Marine Fish Commission Areas (PSMFC); "—" indicates that no information was obtained.

PSMFC area of tagging	PSMFC area of recovery	Days at liberty	Minimum distance displaced (km)	Length at release (cm)	Length at recovery (km)	Injuries at release	Age at recovery (yr)	Sex
Canadian								
3C-US	3B	838	0	44	44	none	15	—
3C-US	3C-US	>3,617	0	44	45	none	—	M
3C-US	3A-3D[1]	N/A	N/A	54	N/A	none	—	—
3C-US	3A	859	125	51	53	none	15	F
3C-US	3C-US	2,577	0	54	N/A	none	—	—
3C-US	3C-US	48	0	53	53	none	—	—
3C-US	3C-US	434	25	46	N/A	bleeding[2]	—	—
3C-US	3C-US	55	0	52	54	none	—	—
3C-US	3C-US	382	0	45	N/A	none	—	—
3C-US	3C-US	2,268	0	45	49	none	—	M
3C-US	3C-US	18	0	43	48	none	—	—
3C-US	4A	1,392	25	45	48	none	—	—
3C-US	3C-US	478	25	47	N/A	none	—	—
3C-CAN	3A	832	125	45	45	loss of scales	13	F
5A+5B	3C-US	1,279	400	42	43	bleeding[3]	11	M
5A+5B	5A+5B	861	25	45	46	none	13	M
5A+5B	3D	3,215	250	42	43	none	—	M
5A+5B	5A+5B	2,119	0	44	48	bleeding[4]	—	M
5A+5B	5A+5B	328	25	46	45	none	20	M
5A+5B	5A+5B	3,219	0	48	48	none	—	M
5A+5B	5A+5B	624	0	51	50	loss of scales	17	M
3C-US	3C-?	1,177	0	49	48	none	—	—
3C-US	2B	690	400	48	45	none	9	F
3C-US	3C-US	73	0	47	N/A	none	—	—
3C-US	3A	798	100	33	39	none	—	M
3C-US	3B	1,218	0	41	46	none	—	M
3C-US	3B	186	0	42	41	none	—	M
3C-US	3A	73	100	46	46	none	—	—
3C-US	3C-US	1,472	0	47	47	none	—	M
3C-US	3A	1,994	100	46	N/A	none	—	—
3C-US	3B	739	0	47	46	none	34	M
3C-US	3C-US	877	0	50	51	none	17	F
3C-US	3C-US	N/A	25	41	39	bruised	—	—
3C-US	3B	1,231	0	48	N/A	none	—	—
3C-US	3C	2,653	0	42	49	none	—	F
3C-US	3A	103	125	42	42	none	—	M
4A	3B	2,438	0	43	46	none	—	M
Alaskan								
SE Alaska	5A+5B	1,827	700	37	45	—	—	—
SE Alaska	3B	2,047	1,400	37	45	—	—	—
SE Alaska	5A+5B	2,842[5]	750	32	N/A	—	—	—
SE Alaska	5A+5B	2,722[6]	625	33	45	—	—	M
SE Alaska	5A+5B	2,729[7]	N/A	41	50	—	—	F

[1] Recovered from Area 3A, 3B, 3C, or 3D.
[2] Bleeding at tag site.
[3] Bleeding at de-gassing site.
[4] Bleeding at oxytetracycline injection site.
[5] 2,842–2,872 days at liberty.
[6] 2,722–3,087 days at liberty.
[7] 2,729–3,094 days at liberty.

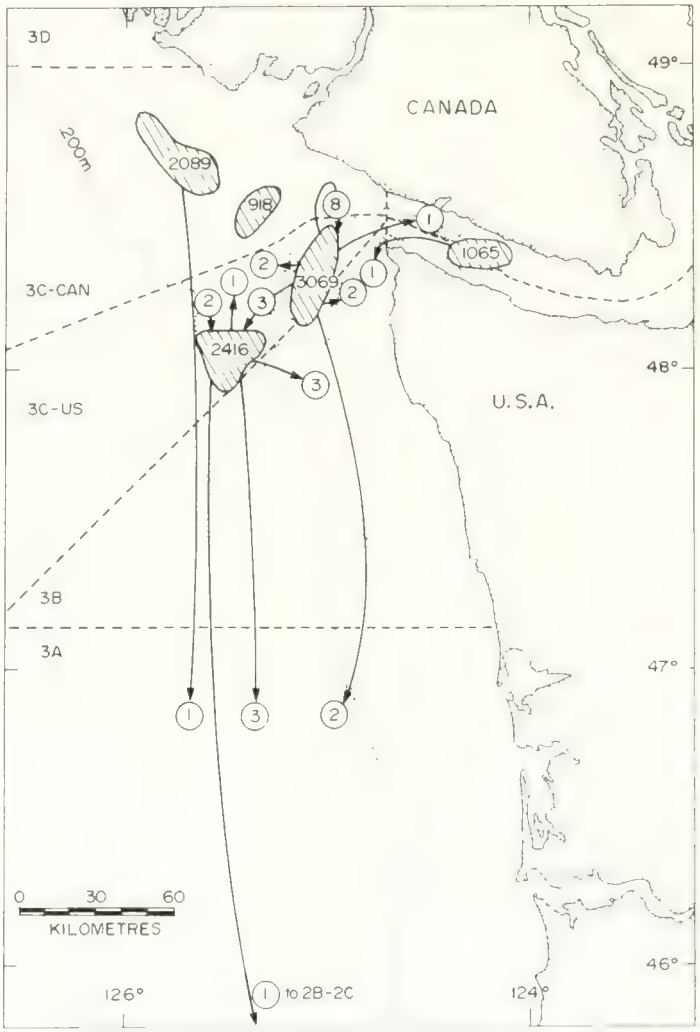

Figure 3

Number of releases (in hatched areas) and recoveries (in circles) of yellowtail rockfish, *Sebastes flavidus*, tagged off southern Vancouver Island and northern Washington (one specimen released in PSMFC area 3C-US was recovered in Areas 2B–2C to the south of the areas shown in this figure).

kan specimens (1.3%) was significantly higher ($P<0.05$) than in the Canadian study (0.26%), even without significant commercial fisheries in the area of release. The average length of all Alaskan-tagged fish was 37 cm (22–56 cm). The average length of recovered fish was 46 cm (45–50 cm). Based on the lengths, the recovered specimens were probably sexually mature when recovered, but probably immature when released.

Discussion

The recoveries of Alaskan specimens are congruent with earlier work, which indicated that immature yellowtail rockfish can make long distance movements (Mathews and Barker, 1983). The Canadian recoveries provide the first evidence that mature yellowtail rockfish can also move significantly longer distances than has been previously reported (Carlson and Haight, 1972; Pearcy, 1992).

The consistent tendency for individuals who travelled away from the release points to be caught farther south along the coast probably resulted from the bias in the distribution of the fishing effort. For the Alaskan and central B.C. releases, there were virtually no fisheries north or west of the release areas. It is surprising that none of the fish tagged in northern

Washington were recovered in Queen Charlotte Sound. However, landings of yellowtail rockfish in Queen Charlotte Sound were also low in the years during, and the first three years following, tagging (Table 4).

The yellowtail rockfish tagged in the Alaskan study were caught in waters shallower than 30 m and were predominantly immature. A southward, ontogenetic migration to the broader continental shelf off central B.C. is possible. This would parallel the movement of immature yellowtail rockfish from Puget Sound to the outer Washington coast (Mathews and Barker, 1983). However, many of these fish may simply move west towards the deeper water on the outer shelf but remain within southeastern Alaska. The limited commercial fishery in these outside waters prevents resolution of these alternatives, although they are not mutually exclusive.

We suggest that the low recovery rate for the Canadian study was caused by short-term post-tagging mortality arising from a combination of the greater depth of capture, the greater stress from trawl capture compared with hook-and-line, and the added handling during anaesthetization, decompression, and OTC injection. The dosage level of OTC may have also contributed to mortality, as studies on other species have shown increasing mortality with dosages greater than 25 mg/kg body weight (McFarlane and Beamish, 1987).

An alternative explanation for low recovery rates in the Canadian study is that the tagged fish were released into very large populations, well in excess of current estimates (Table 4). Thus, landings of 400–900 t in the early 1980's provided little chance for recovery. However, this same logic should then apply to the likelihood of recapturing Alaskan tags in the B.C. fishery at the same time. Since this recovery ratio was much higher, the Alaskan results support the contention of high initial mortality in the Canadian study.

The rate of recovery for Canadian tags was low at the outset and gradually declined over the ten years after release. The 95% confidence limits of the point estimate for the instantaneous rate of decline over the ten years (0.099–0.307) is consistent with the range of extinction rates (0.28–0.54) predicted by combining published estimates of instantaneous rates for natural mortality, 0.06–0.12 (Archibald et al., 1981; Tagart, 1991), tag loss for black rockfish, 0.13 (Lai and Culver, 1991), and fishing mortality for yellowtail rockfish off northern Washington, 0.09–0.29 (Tagart, 1991).

Despite the commercial importance of this species, the stock boundaries are poorly understood. Assessment biologists have resorted to selecting boundaries based on a combination of official statistical areas and on the distribution of major fishing grounds. The most recent assessments have assumed four stocks from groupings of International North Pacific

Table 3

Minimum estimate of years at liberty for yellowtail rockfish, *Sebastes flavidus*, tag recoveries for those with reliable information on recovery date.

Time at liberty (yr)	Number of recoveries	
	Canadian	Alaskan
<1	8	0
1–2	5	0
2–3	7	0
3–4	5	0
4–5	1	0
5–6	2	2
6–7	2	0
7–8	2	3
8–9	2	0
9+	1	0
Total	35	5

Table 4

Landings (t) for 1980–89 and biomass estimates (t) for 1990 of yellowtail rockfish, *Sebastes flavidus*, by region (Stanley, 1991; Tagart, 1991).

Year of landings	SE Alaska	British Columbia[1]	Washington-Oregon-California[2]
1980		704	8,667
1981		426	9,181
1982	1	526	9,184
1983	2	447	9,498
1984	6	353	5,392
1985	5	941	3,449
1986	5	4,458	5,082
1987	8	4,168	5,212
1988	6	4,765	6,193
1989	4	4,298	4,516
1990 Exploitable biomass	unknown	30,000–45,000	20,000–40,000

[1] Northern Vancouver stock biomass partitioned 50% to Washington, 50% B.C.
[2] Does not include the bycatch in offshore fishing for Pacific hake, *Merluccius productus*

Fisheries Commission statistical areas: Charlotte/North Vancouver, South Vancouver, North Columbia, and Eureka/South Columbia (Stanley, 1991; Tagart, 1991) (Fig. 1).

This study does not provide information sufficient to alter the boundaries presently used in stock assessments. However, the clear demonstration of movement for immature and mature yellowtail rockfish should encourage assessment biologists to refine their understanding of stock relationships for this species. This understanding can then be applied to examination of the relative impacts of fishing mortality and potential movements among stock units.

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Literature cited

Archibald, C. P., W. Shaw, and B. M. Leaman.
1981. Growth and mortality estimates of rockfishes (Scorpaenidae) from B.C. coastal waters, 1977–1979. Can. Tech. Rep. Fish. Aquat. Sci. 1048, 57 p.

Carlson, R. H., and R. E. Haight.
1972. Evidence for a home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish. Res. Board Can. 29:1011–1014.

Coombs, C.
1979. Reef fishes near Depoe Bay, Oregon: movement and the recreational fishery. M.A. thesis, Oregon State Univ., Corvallis, 39 p.

Culver, B. N.
1987. Results from tagging black rockfish (*Sebastes melanops*) off the Washington and northern Oregon coast. *In* Proceedings of the international rockfish symposium, p. 231–239. Univ. Alaska Sea Grant Rep. 87-2. Univ. Alaska, Fairbanks, 393 p.

Fadeev, N. S.
1968. Migrations of Pacific ocean perch. Proc. Pac. Sci. Res. Inst. Fish. Ocean. 65:170–177. [Fish. Res. Board Can. Transl. Ser. 1447.]

Gascon, D., and R. A. Miller.
1981. Colonization by nearshore fish on small artificial reefs in Barkley Sound, British Columbia. Can. J. Zool. 59:1635–1646.

Gotshall, D. W.
1964. Increasing tagged rockfish (genus *Sebastodes*) survival by deflating the swim bladder. Calif. Dep. Fish Game, Fish. Bull. 50:253–260.

Gowan, R. E.
1983. Population dynamics and exploitation rates of rockfish (*Sebastes* spp.) in central Puget Sound, Washington. Ph.D. thesis, Univ. Wash., Seattle, 90 p.

Gunderson, D. R.
1971. Evidence that Pacific ocean perch (*Sebastes alutus*) in Queen Charlotte Sound form aggregations that have different biological characteristics. J. Fish. Res. Board Can. 29:1061–1070.

Hartman, A. R.
1987. Movement of scorpionfishes (Scorpaenidae: *Sebastes* and *Scorpaena*) in the southern California Bight. Calif. Dep. Fish Game, Fish. Bull. 73(2):68–79.

Kalbfleisch, J. G.
1976. Probability and statistical inference, Part 2. Univ. Waterloo, Waterloo, Ontario, 307 p.

Lai, H., and B. N. Culver.
1991. Estimation of tag loss rate of black rockfish (*Sebastes melanops*) off the Washington coast with a review of double tagging models. Wash. Dept. Fish. Tech. Rep. 113, 28 p.

Larson, R. J.
1980. Territorial behaviour of the black-and-yellow rockfish and gopher rockfish (Scorpaenidae, *Sebastes*). Mar. Biol. 58:111–122.

Leaman, B. M., and Z. Kabata.
1987. *Neobrachiella robusta* (Wilson, 1912) (Copepoda:Lernaepodidae) as a tag for identification of stocks of its host, *Sebastes alutus* (Gilbert, 1890) (Pisces:Teleostei). Can. J. Zool. 65:2579–2582.

Leaman, B. M., and D. A. Nagtegaal.
1987. Age validation and revised natural mortality rate for yellowtail rockfish. Trans. Am. Fish. Soc. 116:171–175.

Love, M. S.
1980. Isolation of olive rockfish, *Sebastes serranoides*, populations off southern California. Fish. Bull. 77:975–983.

Mathews, S. B., and M. W. Barker.
1983. Movements of rockfish (*Sebastes*) tagged in northern Puget Sound, Washington. Fish. Bull. 81:916–922.

Matthews, K. R., B. S. Miller, and T. P. Quinn.
1987. Movement studies of nearshore demersal rockfishes in Puget Sound, Washington. *In* Proceedings of the international rockfish symposium, p. 63–72. Univ. Alaska Sea Grant Rep. 87–2. Univ. Alaska, Fairbanks, 393 p.

McElderry, H. I.
1979. A comparative study of the movement habits and their relationships to buoyancy compensation in two species of shallow reef rockfish (Pisces: Scorpaenidae). M.Sc. thesis, Univ. Victoria, Victoria, B.C., 168 p.

McFarlane, G. A., and R. J. Beamish.
1987. Selection of dosages of oxytetracycline for age validation studies. Can. J. Fish. Aquat. Sci. 44(4):905–909.

Miller, D. J., and J. J. Geibel.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera,* experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

O'Connell, V. M.
1991. A preliminary examination of breakaway tagging for demersal rockfishes. Alaska Dep. Fish Game, Comm. Fish. Div., Fish. Res. Bull. 91-06, 8 p.

Pearcy, W. G.
1992. Movements of acoustically-tagged yellowtail rockfish *Sebastes flavidus* on Heceta Bank, Oregon. Fish. Bull. 90:726–735.

Shaw, W., D. A. Nagtegaal, C. P. Archibald, and B. M. Leaman.
1981. Rockfish tagging cruises off southwest Vancouver Island (MV *Ocean King*) and off northwest Vancouver Island and in Queen Charlotte Sound (MV *Blue waters*) during 1980. Can. Data Rep. Fish. Aquat. Sci. 288, 133 p.

Stanley, R. D.
1991. Shelf rockfish (silvergray, yellowtail, canary rockfish). *In* J. Fargo, and B. M. Leaman (eds.), Groundfish stock assessments for the west coast of Canada in 1990 and recommended yield options for 1991, p. 225–276. Can. Tech. Fish. Aquat. Sci. 1778.

Tagart, J. V.
1991. Population dynamics of yellowtail rockfish *Sebastes flavidus* stocks in the northern California to southwest Vancouver Island Region. Ph.D. thesis, Univ. Wash., Seattle, 323 p.

Turner, C. H., E. E. Ebert, and R. R. Given.
1969. Man-made reef ecology. Calif. Dep. Fish Game, Fish Bull. 146, 221 p.

Wishard, L. N., F. M. Utter, and D. R. Gunderson.
1980. Stock separation of five rockfish species using naturally occurring biochemical markers. Mar. Fish Rev. 42:64–73.

A simple generalized model of allometry, with examples of length and weight relationships for 14 species of groundfish

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Allometry is a set of relations between an animal's characteristics and its body size, and is applied in many branches of biological sciences including ecology, physiology, and morphology (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Bookstein et al., 1985; Reiss, 1989). Allometry is represented by the power function, $W = AL^{X_2}$, where W is a characteristic of an animal (e.g. body weight), L is its body size, and A and X_2 are its allometric parameters. To determine an allometric relationship for a particular characteristic, the power function is usually, albeit at times inappropriately, double log-transformed into a simple linear equation,

$$Y = X_1 + X_2 X_3, \qquad (1)$$

with $Y = \log(W)$, $X_1 = \log(A)$, and $X_3 = \log(L)$, and is then fit to data from different individuals.

Use of allometry in this way assumes constancy of X_1 and X_2 in Equation 1. While both allometric parameters may be treated approximately as constants in certain applications, the assumption may be violated for a wide variety of biological phenomena because of genetic, phenotypic, and/or behavioral variability among individual animals. In fact, Mosimann and James (1979) have concluded that X_2 varies spatially in the Florida red-winged blackbird, *Agelaius phoeniceus*. Variability in X_2 is also implied in Reiss' (1989) hypothesis that X_2 contains phylogenetic information and is less variable intraspecifically than interspecifically. Peters (1983) convincingly demonstrated interspecific variation in X_2 and computed its mean and standard deviation for metabolic rates scaled to body sizes across many animal taxa. Variability in X_1 has not been examined but is certainly implied in the comprehensive appendices of Peters' (1983) book on the ecological implications of body size and in Reiss' (1989) monograph on the allometry of organismic growth and reproduction. X_1 may be strongly negatively correlated with X_2 for length-weight relationships in fish (e.g. Caillouet, 1993).

Variability in X_1 and X_2 may have major implications in the widely used allometric equation because it represents a fundamental concept in biology (Peters, 1983). In this paper, we generalize Equation 1 by explicitly incorporating variability in and correlation between, X_1 and X_2, and study the consequences of such variability and correlation in allometric predictions. The generalized model is demonstrated by using length and weight relationships for 14 species of groundfish of the families Centrolophidae, Haemulidae, Lethrinidae, Lutjanidae, Nemipteridae, and Synodontidae from northern Australian waters.

Model

Suppose that a joint probability distribution of X_1 and X_2 conditional on X_3 could be formed for a group of animals, with each individual having its own pair of allometric parameters which it retains throughout its life, and that values of pairs of allometric parameters are serially independent. The value of Y for the ith individual with allometric parameter pair (X_{1i}, X_{2i}) at X_3 is

$$Y_i = X_{1i} + X_{2i} X_3.$$

For a group of animals selected randomly from the population, the expected value of Y at X_3 is

$$E[Y \mid X_3] = E[X_1 + X_2 X_3] \qquad (2)$$

with variance

$$\begin{aligned} V[Y \mid X_3] &= V[X_1 + X_2 X_3] \\ &= E[Y^2 \mid X_3] - E[Y \mid X_3]^2 \\ &= E[(X_1 + X_2 X_3)^2] - E[X_1 + X_2 X_3]^2 \end{aligned} \qquad (3)$$

Given information on how X_1 and X_2 vary, one can develop Equations 2 and 3. X_2 may closely follow a normal distribution for metabolic rate of animals scaled to body size (Peters, 1983), being strongly negatively correlated with X_1 for length-weight relationships in fish (e.g. Caillouet, 1993). We will assume below that X_1 and X_2 follow a joint normal distribution, i.e. $(X_1, X_2) \sim N(\mu_1, \mu_2; \sigma_1^2, \sigma_2^2; \rho)$ with mean μ_i, and variance σ_i^2 of X_i, and correlation coefficient ρ. Under general conditions, the sum (or average) of a number of random variables is approximately normally distributed, and such approximation can be quite good even if that number is relatively small. The above assump-

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tion would be at least approximately valid because both X_1 and X_2 can be regarded as the sum (or average) of numerous (e.g. genetic, phenotypic, and behavioral) random components. Analogous models may be developed for other probability distributions. Under that assumption, Equations 2 and 3 become, respectively,

$$\begin{aligned} E[Y \mid X_3] &= E[X_1 + X_2 X_3] \\ &= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \frac{1}{2\pi\sigma_1\sigma_2\sqrt{1-\rho^2}} (x_1 + x_2 X_3) e^{[illegible]} dx_1 dx_2 \\ &= \mu_1 + \mu_2 X_3, \end{aligned} \tag{4}$$

and

$$\begin{aligned} V[Y \mid X_3] &= V[X_1 + X_2 X_3] \\ &= E[Y^2 \mid X_3] - E[Y \mid X_3]^2 \\ &= E[(X_1 + X_2 X_3)^2] - E[X_1 + X_2 X_3]^2 \\ &= \sigma_1^2 + 2\sigma_1\sigma_2\rho X_3 + \sigma_2^2 X_3^2. \end{aligned} \tag{5}$$

Thus variability in, and correlation between, X_1 and X_2 only affect $V[Y \mid X_3]$. $V[Y \mid X_3]$ increases linearly with ρ from $(\sigma_1 - \sigma_2 X_3)^2$ at ρ = –1 through $\sigma_1^2 + \sigma_2^2 X_3^2$ at $\rho = 0$ to $(\sigma_1 + \sigma_2 X_3)^2$ at ρ = 1. It quadratically decreases with σ_1, σ_2, and X_3 to a minimum of $\sigma_2^2 X_3^2 (1-\rho^2) \geq 0$ at $\sigma_1 = -\sigma_2 \rho X_3$, $\sigma_1^2 (1-\rho^2)$ at $\sigma_2 = -\sigma_1 \rho / X_3$ and $\sigma_1^2 (1-\rho^2)$ at $X_3 = -\sigma_1 \rho / \sigma_2$, respectively, and finally increases unboundedly, under the constraint that σ_1, σ_2, and $X_3 \geq 0$. However, if X_1 and X_2 are both deterministic ($\sigma_i^2 = 0, \rho = 0$), $V[Y \mid X_3] = 0$.

If X_1 is random ($\sigma_1^2 > 0$) and X_2 is deterministic ($\sigma_2^2 = 0, \rho = 0$), $V[Y \mid X_3] = \sigma_1^2$. If X_2 is random ($\sigma_2^2 > 0$) and X_1 is deterministic ($\sigma_1^2 = 0, \rho = 0$), $V[Y \mid X_3] = \sigma_2^2 X_3^2$. Finally, if X_1 and X_2 are random but independent ($\sigma_1^2 > 0, \sigma_2^2 > 0$ and $\rho = 0$), $V[Y \mid X_3] = \sigma_1^2 + \sigma_2^2 X_3^2$.

Data and parameter estimation

Data on fish weight at length were collected from Australia's continental shelf in the Timor and Arafura Seas (9–14°S, 127–137°E) from 20 October to 16 December 1990 as part of the Northern Territory Department of Primary Industry and Fisheries' program assessing commercial fish stocks. Of 240 stations allocated randomly within a depth range of 20–200 m, 199 were successfully sampled with a Frank and Bryce trawl net (headline height, 2.9 m; wing spread, 14.4 m; door spread, 60.1 m) at a speed of 1.54–2.06 $m \cdot s^{-1}$. Nearly 48 tonnes of fish representing about 483 species in 119 families were caught during sampling. A representative subsample of individuals of 14 species, mostly of commercial fish, of the families Centrolophidae, Haemulidae, Lethrinidae, Lutjanidae, Nemipteridae, and Synodontidae were frozen immediately on board, returned to the laboratory, thawed, sexed, measured (fork length) to the nearest 1 mm, and weighed (wet weight) to the nearest 1 g with an electronic balance (Mettler, PC4000). For each of the 14 species, data on individual wet weight at length were pooled across all stations and fit to all cases of Equations 4 and 5 for females, males, and mixed sexes. Parameter estimates indicated by hats (^) were obtained by linear regression for Equation 1 by using SAS regression procedure (SAS Institute Inc., 1985) and by maximizing the general likelihood function,

$$L = \prod_{i=1}^{n} \left[2\pi V[Y \mid X_3] + \sigma_e^2 \right]_i^{-\frac{1}{2}} e^{[illegible]},$$

for all other models by using the simplex algorithm of SYSTAT nonlinear regression procedure (Wilkinson, 1989). We included a model error term, σ_e^2, in the likelihood function to show that, in this case, it is compounded with σ_1^2 and is hence equivalent to σ_1^2 and $\sigma_1^2 + \sigma_e^2$ for estimation purposes. For this reason, we treated both error components collectively as 'σ_1^2' during model fitting and result presentation, unless otherwise stated.

Results

Some statistics of fish length and weight data used in this analysis are given in Table 1. We attempted to fit data for mixed sexes (both sexable and unsexable individuals included) and males and females (with unsexable juveniles excluded) of each of 14 species of groundfish to all cases of Equations 4 and 5. However, parameters could be estimated for models with σ_1^2 or σ_2^2 only; those in models simulta-

neously with σ_1^2 and σ_2^2, or simultaneously with σ_1^2, σ_2^2 and ρ could not be estimated because of overparameterization. Estimates of parameters, derived from linear regression of Equation 1 by using least squares method—equivalent to maximizing the likelihood function

$$L = \prod_{i=1}^{n} \left[2\pi\sigma_1^2\right]^{\frac{1}{2}} e^{\frac{[Y_i - E(Y|X_i)]^2}{2\sigma_1^2}}$$

and from maximizing the likelihood function

$$L = \prod_{i=1}^{n} \left[2\pi\sigma_2^2 X_3^2\right]^{\frac{1}{2}} e^{\frac{[Y_i - E(Y|X_3)]^2}{2\sigma_2^2 X_3^2}},$$

are given in Tables 2 and 3 respectively. Estimates in both tables are very similar between sexes for each species and between species, roughly with a species-wide $\hat{\mu}_1 = -10.89$, $\hat{\mu}_2 = 2.99$, $\sigma_1 = -0.006638$ and $\hat{\sigma}_2 = 0.014932$. Thus, while $V[Y|X_3]$ can be treated approximately as a constant, as is usually assumed in previous applications, it does change quadratically with X_3.

Discussion

Peters (1983) observed a large amount of variability in most allometric relationships and recognized a need to identify independent variables of general biological interest other than size. The general model presented in this study takes into account both body size and parameter variability among individual animals in allometric predictions. A major problem in allometry is that allometricians are more apt at providing a statistical description of a new data set than at using their data for hypothesis testing (Peters, 1983). This tendency has led to a plethora of only slightly different allometric equations, none of which can be rejected objectively. Our general model or any of its special cases would form a basis for intrataxal or intertaxal generalizations by treating some of those estimates of allometric parameters as intrataxal or intertaxal variations, hence providing a means for a general "house cleaning" in allometry.

Incorporating more independent variables in allometric modelling may explain more variability in the dependent variable, but it may result in a loss of a basis for comparison between, and manipulation of, allometric equations, such as allometric cancellation (Calder, 1984). The model presented above conforms exactly with conventional allometry and maintains commensuration by its estimated parameter means.

Specification of error structures in allometric models is an essential part of allometric modelling. Errors for Equation 1 are often assumed to be normally distributed with a constant variance, say σ_e^2. Several other interpretations arise from $V[Y|X_3]$ in that, for estimation purposes, σ_e^2 can be interpreted by any combinations of terms on the right-hand side of Equation 5. These and other alternative interpretations may pose problems for some applications. Thus, error structures of an allometric model must be specified cautiously.

There was no gain in precision or accuracy in estimates of allometric parameters in length and weight relationships of some fishes from considering individual variability of allometric parameters. Both Equation 1 and Equations 4 and 5 with σ_1^2 or σ_2^2, alone give an equally adequate description of weight at length data from all 14 species of groundfish concerned. Overparameterization occurred in cases of Equations 4 and 5 simultaneously with σ_1^2 and σ_2^2, or simultaneously with σ_1^2, σ_2^2, and ρ, and, as a result, not all parameters could be estimated from our data. The overparameterization lent further support to this conclusion. Also, although σ_1^2 and σ_2^2 can be estimated separately for each species, they are either equivalent to model error or take such small values (Tables 2 and 3) that $V[Y|X_2]$ can be treated effectively as constant. Finally, when interpreting regression results from various cases of the general model, it should be noted that all other variability will be confounded with, and added to, that of allometric parameters. Our data sets are of moderate sizes (Table 1) and many others of similar size could be expected to behave similarly. Individual variability of allometric parameters probably has a negligible effect on allometric predictions in length and weight relationships of certain fishes. Thus, our work supports the common use of Equation 1 to model intraspecific length and weight relationships in those fishes. However, all parameters in Equations 4 and 5 may be estimable simultaneously for length and weight relationships, as well as for other allometric relationships, if larger data sets or higher taxonomic levels, or both, are used.

A key assumption in our model is that the independent characteristic, L, (e.g. length) has little measurement error relative to the dependent characteristic, W (e.g. weight). Theoretically, this may not be the case. However, we believe that our model will provide good approximations for many allometrically scaled phenomena, such as length and weight relationships in certain fishes. For other allometric phenomena, alternative formulations, such as those of Pienaar and Ricker (1968), Saenger (1989), Seim and Saether (1983), and Shoesmith (1990) may be useful.

$V[Y|X_3]$ is a function of the independent variable whenever there is individual variability in X_2 or in X_1 and X_2. If this is not taken into account in regres-

Table 1

Some statistics of length and weight data for mixed sexes (both sexable and unsexable individuals included), males and females (with unsexable juveniles excluded) of each of 14 species of groundfish caught in northern Australian waters during 20 October to 16 December 1990.

			Fork length (mm)				Body weight (g)			
Sex	Species	*n*	Mean	SD	Min	Max	Mean	SD	Min	Max
Mixed										
Diagramma pictum	painted sweetlip	413	374.753	135.174	127	610	1,044.94	906.31	27	3,415
Lethrinus fraenatus	blue-lined emperor	48	344.562	63.134	201	450	907.77	469.80	165	1,837
Lethrinus lentjan	red-spot emperor	334	278.521	43.792	190	430	457.04	234.31	143	1,567
Lutjanus erythropterus	scarlet snapper	172	431.105	54.429	255	536	1,269.63	417.65	255	2,373
Lutjanus malabaricus	saddle-tailed snapper	590	377.398	151.595	86	765	1,170.71	1074.90	13	7,251
Lutjanus sebae	red emperor	182	342.346	125.237	94	596	1,144.50	974.22	18	4,736
Lutjanus timorensis	Timor snapper	43	415.256	38.608	211	453	1,339.72	271.27	178	1,663
Lutjanus vittus	one-band snapper	450	188.364	30.864	98	300	114.65	59.41	15	461
Nemipterus furcosus	rosy threadfin-bream	479	164.382	34.187	38	250	95.61	55.97	3	300
Nemipterus hexodon	ornate threadfin-bream	479	149.714	28.517	93	230	73.35	44.00	15	252
Pristipomoides multidens	gold-band snapper	293	314.055	117.079	131	585	818.53	882.70	50	3,800
Pristipomoides typus	sharp-tooth snapper	131	207.130	106.140	87	550	302.01	540.41	12	2,705
Psenopsis humerosa	black-spot butterfish	254	158.106	14.633	105	195	106.74	32.23	25	202
Saurida micropectoralis	short-finned lizardfish	444	261.218	34.039	110	410	194.26	90.32	12	850
Female										
Diagramma pictum	painted sweetlip	185	405.827	118.834	185	610	1,192.71	847.30	88	3,377
Lethrinus fraenatus	blue-lined emperor	32	318.031	48.035	201	445	690.22	313.06	165	1,757
Lethrinus lentjan	red-spot emperor	255	265.435	35.665	194	422	389.43	185.90	146	1,567
Lutjanus erythropterus	scarlet snapper	78	430.731	43.480	345	536	1,285.32	402.82	627	2,373
Lutjanus malabaricus	saddle-tailed snapper	193	472.637	90.217	175	716	1,702.28	811.06	89	5,196
Lutjanus sebae	red emperor	88	386.159	86.001	197	535	1,357.81	791.64	155	3,176
Lutjanus timorensis	Timor snapper	25	414.520	22.417	378	451	1,320.64	207.65	978	1,663
Lutjanus vittus	one-band snapper	212	181.835	24.025	120	262	100.01	41.03	29	289
Nemipterus furcosus	rosy threadfin-bream	240	161.429	25.781	38	230	85.36	40.47	7	239
Nemipterus hexodon	ornate threadfin-bream	270	146.463	23.825	97	208	67.34	33.01	18	176
Pristipomoides multidens	gold-band snapper	98	356.735	117.750	180	585	1,103.23	1,001.25	108	3,800
Pristipomoides typus	sharp-tooth snapper	29	287.034	111.650	135	550	593.48	720.46	42	2,705
Psenopsis humerosa	black-spot butterfish	101	167.050	12.046	138	195	126.50	30.13	61	202
Saurida micropectoralis	short-finned lizardfish	164	284.860	36.753	197	410	256.20	111.99	71	850
Male										
Diagramma pictum	painted sweetlip	119	448.303	111.902	177	594	1,528.94	917.86	77	3415
Lethrinus fraenatus	blue-lined emperor	16	397.625	56.707	216	450	1,342.88	431.39	191	1837
Lethrinus lentjan	red-spot emperor	74	325.743	35.281	220	430	698.30	229.21	202	1469
Lutjanus erythropterus	scarlet snapper	93	433.312	59.850	258	535	1,267.23	421.10	255	2233
Lutjanus malabaricus	saddle-tailed snapper	200	449.215	122.859	183	765	1,622.40	1,121.62	105	7251
Lutjanus sebae	red emperor	45	423.822	94.510	187	596	1,772.42	1,048.84	124	4736
Lutjanus timorensis	Timor snapper	17	428.353	19.193	388	453	1,436.12	183.58	1,021	1613
Lutjanus vittus	one-band snapper	225	197.858	31.901	128	300	132.84	67.83	32	461
Nemipterus furcosus	rosy threadfin-bream	205	178.800	30.351	115	250	120.09	61.04	28	300
Nemipterus hexodon	ornate threadfin-bream	125	165.832	32.361	107	230	99.21	58.00	20	252
Pristipomoides multidens	gold-band snapper	127	333.276	108.795	141	580	897.81	840.95	60	3,475
Pristipomoides typus	sharp-tooth snapper	35	267.314	99.371	114	530	477.31	581.00	27	2,617
Psenopsis humerosa	black-spot butterfish	117	153.821	13.416	105	191	97.19	26.08	25	198
Saurida micropectoralis	short-finned lizardfish	263	249.433	19.805	186	295	161.19	41.16	63	289

sion analysis, too much weight would be given to observations of the dependent variable in the region with high variances, and the analysis will be overly sensitive to chance events or bias affecting observations in this region of the independent variable.

Length and weight relationships in fishes are often required for stock assessment and for intra- and inter-specific comparisons. Although many data are available on weight at length relationships of fishes from New Guinea (Showers, 1993) and New Cale-

Table 2

Estimates of mean and standard error of allometric parameters obtained for mixed sexes, males, and females of each of 14 species of groundfish, caught in northern Australian waters during 20 October to 16 December 1990 by linear regression of Equation 1 by using least squares method. $P \leq 0.0001$ applies to all species for separate sexes.

	Mixed					
Species[1]	$\hat{X}_1$ (SE)	$\hat{X}_2$ (SE)	$n-2$	$F_{1,n-2}$	P	R^2
Diagramma pictum	−11.4249 (0.0650)	3.0427 (0.0111)	411	75,363.608	0.0000	0.9946
Lethrinus fraenatus	−11.1084 (0.2933)	3.0501 (0.0503)	46	3,673.450	0.0001	0.9874
Lethrinus lentjan	−10.8678 (0.1287)	3.0049 (0.0229)	332	17,226.485	0.0001	0.9810
Lutjanus erythropterus	−10.2265 (0.2323)	2.8569 (0.0383)	170	5,550.516	0.0001	0.9701
Lutjanus malabaricus	−10.4713 (0.0478)	2.8926 (0.0082)	588	125,849.921	0.0000	0.9953
Lutjanus sebae	−10.7588 (0.0752)	2.9931 (0.0130)	180	52,732.028	0.0001	0.9966
Lutjanus timorensis	−10.2548 (0.5172)	2.8916 (0.0858)	41	1,134.654	0.0001	0.9643
Lutjanus vittus	−10.5972 (0.0985)	2.9136 (0.0188)	448	23,905.566	0.0000	0.9816
Nemipterus furcosus	−10.6433 (0.1163)	2.9552 (0.0229)	477	16,672.088	0.0000	0.9721
Nemipterus hexodon	−10.8475 (0.1277)	3.0010 (0.0256)	477	13,778.375	0.0000	0.9665
Pristipomoides multidens	−10.4284 (0.0629)	2.9192 (0.0110)	291	69,881.156	0.0000	0.9958
Pristipomoides typus	−10.6474 (0.0672)	2.9462 (0.0128)	129	52,895.132	0.0001	0.9975
Psenopsis humerosa	−11.8119 (0.2644)	3.2487 (0.0523)	252	3,863.670	0.0001	0.9385
Saurida micropectoralis	−12.3581 (0.1948)	3.1560 (0.0351)	442	8,106.551	0.0001	0.9482
	Female					
Species[1]	$\hat{X}_1$ (SE)	$\hat{X}_2$ (SE)	$n-2$	$F_{1,n-2}$	R^2	
Diagramma pictum	−11.4854 (0.1323)	3.0526 (0.0222)	183	18,940.693	0.9904	
Lethrinus fraenatus	−10.9359 (0.4586)	3.0204 (0.0797)	30	1,435.635	0.9788	
Lethrinus lentjan	−11.0141 (0.1823)	3.0314 (0.0327)	253	8,591.353	0.9713	
Lutjanus erythropterus	−11.1443 (0.3965)	3.0123 (0.0654)	76	2,120.223	0.9649	
Lutjanus malabaricus	−10.6937 (0.1855)	2.9290 (0.0302)	191	9,397.044	0.9800	
Lutjanus sebae	−10.9484 (0.2014)	3.0256 (0.0339)	86	7,943.456	0.9892	
Lutjanus timorensis	−8.5750 (1.6316)	2.6136 (0.2708)	23	93.182	0.7934	
Lutjanus vittus	−10.4418 (0.1823)	2.8824 (0.0351)	210	6,752.525	0.9697	
Nemipterus furcosus	−9.0380 (0.2490)	2.6379 (0.0491)	238	2,888.362	0.9236	
Nemipterus hexodon	−10.5120 (0.1626)	2.9366 (0.0327)	268	8,081.145	0.9678	
Pristipomoides multidens	−10.4544 (0.1318)	2.9235 (0.0226)	96	16,739.747	0.9942	
Pristipomoides typus	−10.3553 (0.1890)	2.8933 (0.0337)	27	7,358.630	0.9962	
Psenopsis humerosa	−12.0558 (0.5391)	3.2969 (0.1054)	99	978.916	0.9072	
Saurida micropectoralis	−12.4764 (0.3404)	3.1777 (0.0603)	162	2,777.965	0.9446	
	Male					
Species[1]	$\hat{X}_1$ (SE)	$\hat{X}_2$ (SE)	$n-2$	$F_{1,n-2}$	R^2	
Diagramma pictum	−11.8373 (0.1399)	3.1102 (0.0230)	117	18,239.181	0.9936	
Lethrinus fraenatus	−11.5601 (0.5382)	3.1252 (0.0901)	14	1,204.055	0.9877	
Lethrinus lentjan	−11.1870 (0.3227)	3.0589 (0.0558)	72	3,002.105	0.9763	
Lutjanus erythropterus	−9.9051 (0.2875)	2.8006 (0.0474)	91	3,487.397	0.9743	
Lutjanus malabaricus	−10.6166 (0.1268)	2.9171 (0.0209)	198	19,525.208	0.9899	
Lutjanus sebae	−11.5487 (0.2166)	3.1216 (0.0359)	43	7,544.416	0.9942	
Lutjanus timorensis	−9.4597 (1.8694)	2.7597 (0.3085)	15	80.011	0.8316	
Lutjanus vittus	−10.5218 (0.1447)	2.9007 (0.0274)	223	11,186.525	0.9804	
Nemipterus furcosus	−10.9360 (0.1538)	3.0150 (0.0297)	203	10,282.691	0.9805	
Nemipterus hexodon	−10.9499 (0.2803)	3.0188 (0.0550)	123	3,011.431	0.9604	
Pristipomoides multidens	−10.3481 (0.1032)	2.9054 (0.0179)	125	26,357.314	0.9952	
Pristipomoides typus	−10.3289 (0.1707)	2.8902 (0.0308)	33	8,794.451	0.9961	
Psenopsis humerosa	−10.6433 (0.3927)	3.0174 (0.0780)	115	1,495.187	0.9280	
Saurida micropectoralis	−11.6679 (0.4003)	3.0307 (0.0726)	261	1,744.792	0.8694	

[1] See Table 1 for common names.

Table 3

Estimates of mean and asymptotic standard error (ASE) of allometric parameters obtained for mixed sexes, males, and females of each of 14 species of groundfish, caught in northern Australian waters during 20 October to 16 December 1990 by fitting Equations 4 and 5 with $V[Y|X_3] = \sigma_2^2 X_3^2$ excluding the model error term (σ_e^2).

	Mixed		
Species[1]	$\hat{\mu}_1$ (ASE)	$\hat{\mu}_2$ (ASE)	$\hat{\sigma}_2$ (ASE)
Diagramma pictum	−11.4010 (0.0624)	3.0386 (0.0107)	0.015684 (0.000536)
Lethrinus fraenatus	−11.0788 (0.2791)	3.0450 (0.0480)	0.011364 (0.001120)
Lethrinus lentjan	−10.8528 (0.1295)	3.0022 (0.0231)	0.011431 (0.000427)
Lutjanus erythropterus	−10.2207 (0.2246)	2.8559 (0.0371)	0.011478 (0.000598)
Lutjanus malabaricus	−10.4315 (0.0455)	2.8858 (0.0079)	0.015562 (0.000445)
Lutjanus sebae	−10.7324 (0.0705)	2.9885 (0.0124)	0.013522 (0.000691)
Lutjanus timorensis	−10.3142 (0.4613)	2.9015 (0.0766)	0.010599 (0.001097)
Lutjanus vittus	−10.5948 (0.0968)	2.9132 (0.0186)	0.012502 (0.000405)
Nemipterus furcosus	−10.3566 (0.1275)	2.8986 (0.0252)	0.028576 (0.000918)
Nemipterus hexodon	−10.8451 (0.1281)	3.0006 (0.0257)	0.021340 (0.000683)
Pristipomoides multidens	−10.4311 (0.0626)	2.9196 (0.0111)	0.012057 (0.000483)
Pristipomoides typus	−10.6917 (0.0692)	2.9547 (0.0134)	0.012299 (0.000737)
Psenopsis humerosa	−11.8293 (0.2619)	3.2521 (0.0518)	0.015465 (0.000673)
Saurida micropectoralis	−12.3549 (0.1919)	3.1555 (0.0346)	0.017171 (0.000567)
	Female		
Species[1]	$\hat{\mu}_1$ (ASE)	$\hat{\mu}_2$ (ASE)	$\hat{\sigma}_2$ (ASE)
Diagramma pictum	−11.4694 (0.1271)	3.0499 (0.0214)	0.016512 (0.000844)
Lethrinus fraenatus	−10.8822 (0.4288)	3.0111 (0.0747)	0.011972 (0.001450)
Lethrinus lentjan	−10.9932 (0.1843)	3.0276 (0.0331)	0.011992 (0.000515)
Lutjanus erythropterus	−11.1343 (0.3913)	3.0106 (0.0646)	0.009438 (0.000718)
Lutjanus malabaricus	−10.6957 (0.1742)	2.9293 (0.0284)	0.015106 (0.000754)
Lutjanus sebae	−10.9216 (0.1938)	3.0211 (0.0328)	0.013024 (0.000956)
Lutjanus timorensis	−8.5443 (1.5702)	2.6085 (0.2606)	0.011468 (0.001567)
Lutjanus vittus	−10.4305 (0.1808)	2.8802 (0.0348)	0.012749 (0.000602)
Nemipterus furcosus	−8.0532 (0.2559)	2.4435 (0.0506)	0.030733 (0.001396)
Nemipterus hexodon	−10.4947 (0.1627)	2.9332 (0.0328)	0.017758 (0.000753)
Pristipomoides multidens	−10.4486 (0.1296)	2.9225 (0.0224)	0.012449 (0.000864)
Pristipomoides typus	−10.3916 (0.1853)	2.8998 (0.0333)	0.011512 (0.001461)
Psenopsis humerosa	−12.0680 (0.5276)	3.2992 (0.1032)	0.015033 (0.001037)
Saurida micropectoralis	−12.4710 (0.3370)	3.1768 (0.0598)	0.017557 (0.000955)
	Male		
Species[1]	$\hat{\mu}_1$ (ASE)	$\hat{\mu}_2$ (ASE)	$\hat{\sigma}_2$ (ASE)
Diagramma pictum	−11.7895 (0.1296)	3.1023 (0.0214)	0.012092 (0.000760)
Lethrinus fraenatus	−11.5461 (0.4630)	3.1229 (0.0776)	0.009625 (0.001619)
Lethrinus lentjan	−11.1988 (0.3127)	3.0609 (0.0541)	0.009055 (0.000704)
Lutjanus erythropterus	−9.9036 (0.2774)	2.8003 (0.0458)	0.011754 (0.000834)
Lutjanus malabaricus	−10.5854 (0.1203)	2.9120 (0.0199)	0.014870 (0.000728)
Lutjanus sebae	−11.5462 (0.2006)	3.1212 (0.0334)	0.009834 (0.000989)
Lutjanus timorensis	−9.4896 (1.7559)	2.7646 (0.2898)	0.008735 (0.001411)
Lutjanus vittus	−10.5171 (0.1433)	2.8998 (0.0272)	0.012371 (0.000566)
Nemipterus furcosus	−10.9048 (0.1524)	3.0089 (0.0295)	0.014279 (0.000690)
Nemipterus hexodon	−10.9325 (0.2732)	3.0153 (0.0538)	0.023605 (0.001481)
Pristipomoides multidens	−10.3460 (0.1004)	2.9051 (0.0175)	0.011230 (0.000680)
Pristipomoides typus	−10.3560 (0.1709)	2.8951 (0.0311)	0.010902 (0.001254)
Psenopsis humerosa	−10.6920 (0.3878)	3.0271 (0.0771)	0.014853 (0.000951)
Saurida micropectoralis	−11.6947 (0.3976)	3.0356 (0.0721)	0.016898 (0.000725)

[1] See Table 1 for common names.

donia (Kulbicki et al., 1993), systematic data are lacking from northern Australian waters. Because our data covered relatively large size ranges of each of the 14 species of fish concerned, our estimates of allometric parameters and associated relationships will improve stock assessments of major groundfish in northern Australian waters.

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Literature Cited

Bookstein, F. L., B. Chernoff, R. L. Elder, J. M. Humphries, Jr., G. R. Smith and R. E. Strauss.
1985. Morphometrics in evolutionary biology: the geometry of size and shape change, with examples from fishes. Special Publication 15, The Academy of Natural Sciences of Philadelphia, 277 p.

Caillouet, C. W., Jr.
1993. On comparing groups of fishes based on length-weight relationships. NAGA, The ICLARM Quarterly 16:30–31.

Calder, W. A.
1984. Size, function, and life history. Harvard Univ. Press, Cambridge, MA, 431 p.

Kulbicki, M., G. Mou Tham, P. Thollot, and L. Wantiez.
1993. Length-weight relationships of fish from the lagoon of New Caledonia. NAGA, The ICLARM Quarterly 16:26–30.

Mosimann, J. E., and F. C. James.
1979. New statistical methods for allometry with application to Florida red-winged blackbirds. Evolution 33:444–459.

Peters, R. E.
1983. The ecological implications of body size. Cambridge Univ. Press, Cambridge, 329 p.

Pienaar, L. V., and W. E. Ricker.
1968. Estimating mean weight from length statistics. J. Fish. Res. Board Can. 25:2743–2747.

Reiss, M. J.
1989. The allometry of growth and reproduction. Cambridge Univ. Press, Cambridge, England, 182 p.

Saenger, R. A.
1989. Bivariate normal swimbladder size allometry models and allometric exponents for 38 mesopelagic swimbladdered fish species commonly found in the North Sargasso Sea. Can. J. Fish. Aquat. Sci. 46:1986–2002.

SAS Institute, Inc.
1985. SAS user's guide, Version 5. SAS Institute, Cary, NC, 956 p.

Schmidt-Nielsen, K.
1984. Scaling: why is animal size so important? Cambridge Univ. Press, Cambridge, 241 p.

Seim, E., and B. Saether
1983. On rethinking allometry: which regression model to use? J. Theor. Biol. 104:161–168.

Shoesmith, E.
1990. A comparison of methods for estimating mean fecundity. J. Fish. Biol. 36:73–84.

Showers, P. A. T.
1993. Length-weight relationships of five species of the family Sparidae in the Gulf of New Guinea. NAGA, The ICLARM Quarterly 16:32–33.

Wilkinson, L.
1989. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, IL, 638 p.

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Abstract.—The reproductive biology of Atlantic croaker, *Micropogonias undulatus*, collected during 1990–91 from commercial catches in Chesapeake Bay and in Virginia and North Carolina coastal waters (n=3,091), was studied by using macroscopic and microscopic gonad staging, the gonadosomatic index, oocyte diameter distributions, and histological analysis. Atlantic croaker are multiple spawners with asynchronous oocyte development and indeterminate fecundity. Mean length at first maturity for males and females was 182 and 173 mm TL, respectively. More than 85% of both sexes were mature by the end of their first year and all were mature by age 2. Spawning extends over a protracted period (July–December), but individual fish apparently spawn over a shorter interval. Eleven gravid and running-ripe females were collected within the Chesapeake Bay suggesting some spawning occurs in estuarine waters. Monthly sex ratios indicated a strong predominance of females during the main period of spawning. A high incidence of atretic, advanced yolked oocytes in spawning females collected throughout the spawning season suggests that a surplus production of yolked oocytes may be part of the reproductive strategy of Atlantic croaker.

Maturity, spawning, and ovarian cycle of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters*

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The Atlantic croaker, *Micropogonias undulatus* (Linnaeus), ranges from Cape Cod, Massachusetts, to the Bay of Campeche, Mexico (Welsh and Breder, 1923; Johnson, 1978). Although not common north of New Jersey (Hildebrand and Schroeder, 1928; McHugh, 1981), it is one of the most abundant inshore, demersal species of the Atlantic and Gulf of Mexico coasts of the United States (Joseph, 1972).

Despite the large number of studies describing spawning periodicity of Atlantic croaker in the mid-Atlantic and Chesapeake regions (e.g. Hildebrand and Schroeder, 1928; Wallace, 1940; Johnson, 1978; Colton et al., 1979; Morse, 1980; Norcross and Austin, 1988), studies on reproductive biology are rare and mostly incomplete. Information on sexual maturity, fecundity, and sex ratios has been reported (Hildebrand and Schroeder, 1928; Wallace, 1940; Morse, 1980). However, speculation on whether or not Atlantic croaker spawn within Chesapeake Bay (Welsh and Breder, 1923; Pearson, 1941; Haven, 1957) has not been investigated; estimates of size at maturity (Wallace, 1940; Morse, 1980) do not agree; estimates of age at maturity (Welsh and Breder, 1923; Wallace, 1940) were based on length frequency and scale ageing, which have been shown to be less accurate than otolith ageing for Atlantic croaker (Joseph, 1972; Barbieri et al., 1994); and available fecundity estimates (Morse, 1980) cannot be used without an evaluation of Atlantic croaker's fecundity pattern, i.e. whether they have determinate or indeterminate annual fecundity.

Traditionally, estimates of fish fecundity have been based on the assumption that the total number of eggs spawned by a female each year (annual fecundity) is fixed prior to the onset of spawning, a condition known as determinate fecundity (Hunter et al., 1992). However, recent evidence (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985a; Hunter et al., 1985; Horwood and Greer Walker, 1990) indicates that in many temperate and tropical fish annual fecundity cannot be estimated from the standing stock of advanced oocytes because unyolked oocytes continue to be matured and spawned through-

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out the spawning season. This condition is called indeterminate fecundity (Hunter et al., 1992). The only way to estimate annual fecundity, therefore, is by estimating batch fecundity—the number of eggs released during each spawning—and multiplying it by spawning frequency—the number of times an average female spawns during the spawning season (Hunter and Macewicz, 1985a; Hunter et al., 1985, 1992). Although the extended spawning season of Atlantic croaker (Wallace, 1940; Colton et al., 1979; Warlen, 1982) suggests it is a multiple spawner with indeterminate fecundity, no attempt has been made to evaluate its fecundity pattern.

In this study we test the assumption of determinate annual fecundity and describe spawning periodicity, size and age at maturity, sex ratios, ovarian cycle, and oocyte atresia for Atlantic croaker in the Chesapeake Bay and adjacent coastal waters.

Methods

Four approaches were used to sample Atlantic croaker for this study. In 1990 and 1991 fish were collected from commercial poundnet, haul-seine, and gillnet fisheries that operate from late spring to early fall in the lower Chesapeake Bay (Fig. 1). Local fish processing houses and seafood dealers were contacted weekly during April–October 1990 and 1991, and one 22.7 kg (50 lb) box of fish of each available market grade (small, medium, or large) was purchased for processing. Since Atlantic croaker migrate out of Chesapeake Bay in midfall to overwinter offshore (Haven, 1959), monthly samples from November to March 1990 and from November through December 1991 were obtained from commercial trawlers operating in Virginia and North Carolina shelf waters. In addition to these collections, daily samples from a gill net in the lower York River were obtained during the periods August–October 1990 and July–October 1991, except on weekends. In 1991 the net was emptied twice a day: in the early morning (6:00–8:00 am) and in the evening (5:00–7:00 pm). Time of death was recorded for fish alive at the time the net was emptied. Daily gillnet samples were used to monitor small-scale (less than weekly) changes in Atlantic croaker reproductive condition and to collect hydrated or recently spawned females. Finally, collections from the commercial fisheries were supplemented by fish obtained from the Virginia Institute of Marine Science (VIMS) juvenile bottom trawl survey. The VIMS trawl survey used a monthly stratified random sampling program in the lower Chesapeake Bay and monthly

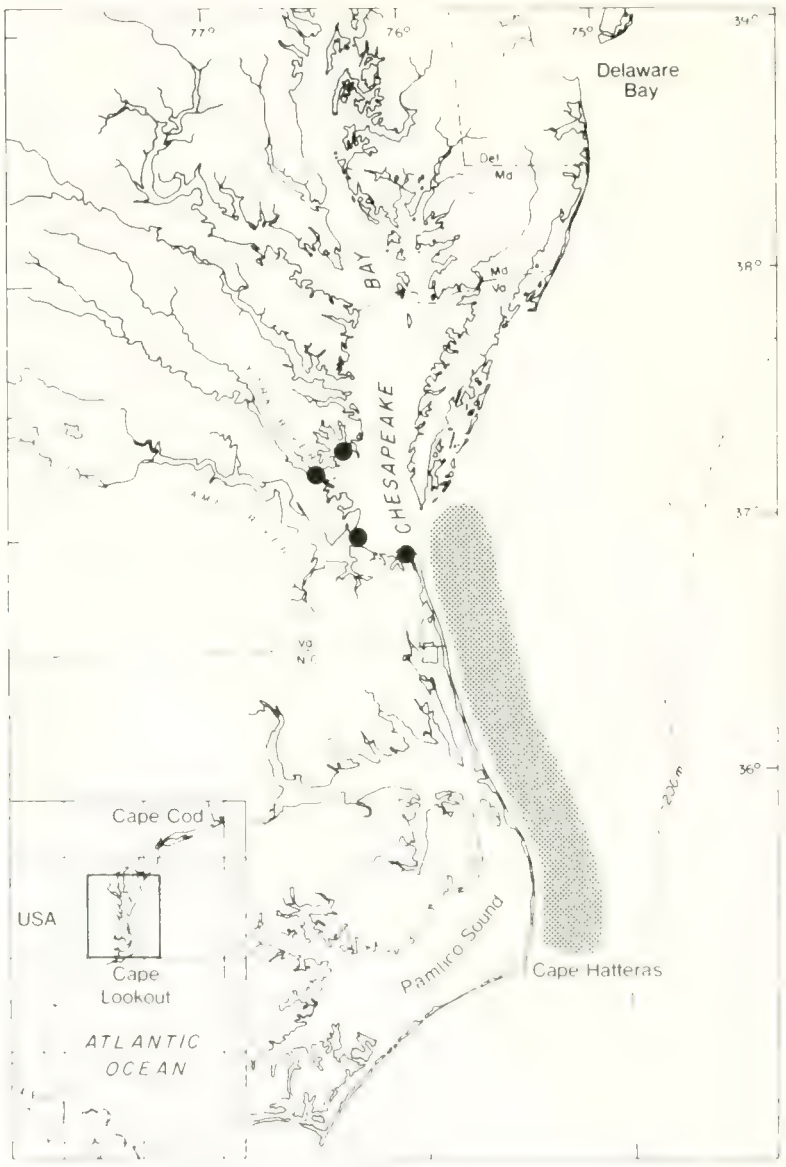

Figure 1

Map of the Chesapeake Bay and mid-Atlantic region. Black dots in Chesapeake Bay indicate poundnet, haul-seine, or gillnet collection sites. Hatched area off Virginia and North Carolina indicates where otter trawl collections of Atlantic croaker, *Micropogonias undulatus*, were obtained.

fixed midchannel stations in the York, James, and Rappahannock rivers.

Fish were measured for total length (TL, ±1.0 mm), total weight (TW, ±1.0 g), and gonad weight (GW, ±1.0 mm), sexed, and both sagittal otoliths were removed and stored dry. The left otolith was sectioned through the core with the diamond blade of a Buehler low-speed Isomet saw. Sections 350–500 µm thick were then mounted on glass slides with Flo-texx clear mounting medium and aged under a dissecting microscope (6–12×) following criteria described in Barbieri et al. (1994). The gonadosomatic index (GSI) was calculated for individual fish as (GW/(TW–GW)·100). Females were assigned a macroscopic gonad maturity stage (Table 1). Males were classified only as sexually mature or immature. Female macroscopic stages were verified microscopically by inspecting fresh oocyte samples and histology slides of a randomly selected subsample of ovaries in each maturity stage. Fresh oocytes were removed from one ovary, spread on a microscope slide, and examined under a dissecting microscope (12–50×). Color photographs were used to permanently record the appearance of fresh oocyte samples. This technique allowed fresh oocytes to be compared with histology slides in assessing gonad maturity stage and the

Table 1

Description of gonad maturity stages for female Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters. Macroscopic appearance refers to fresh ovaries. Gonad stages 3, 4, and 5 are in spawning phase. FOM = final oocyte maturation; POF's = postovulatory follicles.

Stage	Macroscopic appearance	Microscopic appearance
(1) Immature	Ovaries very small, light pink in color; translucent.	Only primary growth oocytes present; no atresia; ovarian membrane thin.
(2) Developing	Ovaries ranging from small to medium (≤ 25% of body cavity); yellow to light orange in color; no opaque (advanced yolked) oocytes present.	Only primary growth, cortical alveoli and a few partially yolked oocytes present; no major atresia.
(3) Fully developed	Ovaries ranging from large (25–50% of body cavity) to very large (~100% of space available in body cavity); creamy yellow to orange in color; opaque oocytes prevalent and easily detected; if partially spent, may have some left-over clear (hydrated) oocytes present at the posterior end of the ovarian lumen.	Primary growth to advanced yolked oocytes present; may have some left-over hydrated oocytes from previous spawning; often major atresia of advanced yolked oocytes, but no major atresia of other oocytes.
(4) Gravid	Ovaries ranging from large (25–50% of body cavity) to very large (~100% of space available in body cavity); creamy yellow to light orange in color; unovulated clear (hydrated) oocytes visible amongst opaque oocytes, giving a speckled appearance; clear oocytes not collected in the ovarian lumen.	Primary growth to FOM/hydrated oocytes present; often major atresia of advanced yolked oocytes, but no major atresia of other oocytes; hydrated oocytes are still in follicles (unovulated).
(5) Running-ripe	Ovaries ranging from large (25–50% of body cavity) to very large (~100% of space available in body cavity); creamy yellow to light orange in color; most clear (hydrated) oocytes are collected in the ovarian lumen (ovulated).	Primary growth to FOM/hydrated oocytes present; often major atresia of advanced yolked oocytes, but no major atresia of other oocytes; hydrated oocytes not in follicles (ovulated); may have POF's.
(6) Regressing	Ovaries ranging from small to medium (≤25% of body cavity); mustard yellow to light orange in color; more flaccid than previous stages; often contain clear fluid; can detect a few opaque oocytes.	Primary growth to advanced yolked oocytes present, but the number of yolked oocytes relative to unyolked oocytes is now much smaller; major atresia of cortical alveoli, partially yolked and advanced yolked oocytes.
(7) Resting	Ovaries very small; dark orange to reddish in color; no opaque oocytes present; ovarian membrane thickened and more opaque than in immature fish.	The majority (>90%) of oocytes are primary growth; may have other oocytes in late stages of atresia; more follicular tissue than immature fish.

occurrence and intensity of oocyte atresia. For histological preparation, tissue samples were fixed in 10% neutrally buffered formalin for 24 hours, soaked in water another 24 hours, and stored in 70% ethanol. Samples were embedded in paraffin, sectioned to 5–6 µm thickness and stained with Harris' Hematoxylin and Eosin Y. Histological classification of ovaries (Table 1) was based on the occurrence and relative abundance of five stages of oocyte development (primary growth, cortical alveoli, partially yolked, advanced yolked, and hydrated) and on the occurrence and intensity of alpha (α) atresia. Terminology for stages of oocyte development and ovarian atresia follows Wallace and Selman (1981), Hunter and Macewicz (1985b) and Hunter et al. (1992).

Fecundity pattern was evaluated through monthly oocyte diameter distributions of fully developed (gonad stage 3) females collected during the spawning season. Before measurements were taken, oocytes were hydraulically separated from each other and from the ovarian membrane and preserved in 2% formalin following the method of Lowerre-Barbieri and Barbieri (1993). Oocyte measurements were taken after a preservation period of at least 24 hours. Samples were stirred before oocytes were removed to reduce bias from settling differences caused by oocyte size or density. Oocytes ≥0.1 mm were measured (±0.02 mm) with an ocular micrometer in a dissecting microscope. Measurements were taken along the median axis of the oocyte parallel to the horizontal micrometer gradations (Macer, 1974; DeMartini and Fountain, 1981).

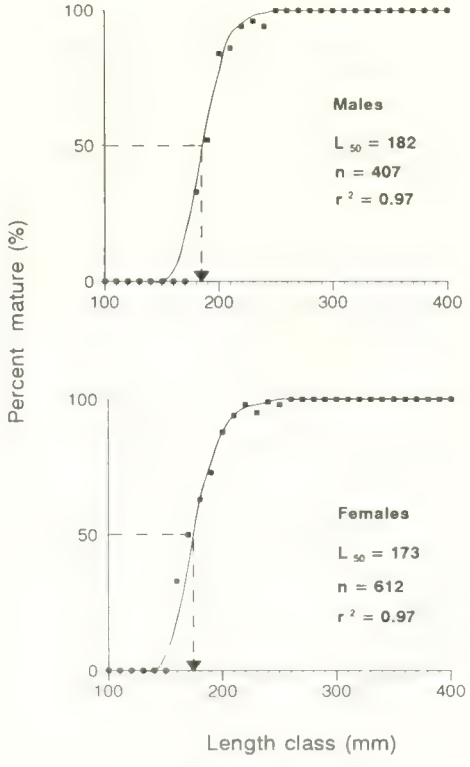

Figure 2

Percentage of mature male and female Atlantic croaker, *Micropogonias undulatus*, by 10-mm total length intervals, with a logistic function (continuous line) fitted to the data. Arrows indicate mean length at first maturity (L_{50}). *n*=sample size.

To estimate mean length at first maturity (L_{50}) for males and females, the fraction of mature fish per 10 mm length intervals was fit to the logistic function by nonlinear regression (Marquardt method), by using the statistical software program FISHPARM (Saila et al., 1988). L_{50} was defined as the smallest length interval in which 50% of the individuals were sexually mature. Females were considered sexually mature if they were in gonad stage 2 (developing) or higher (Table 1). However, to avoid classifying resting (reproductively inactive) or early developing fish as immature, and thus obtaining biased estimates of L_{50}, only fish collected in September, when no resting or developing stages were found, were used for this analysis.

Monthly sex ratios were tested statistically for significant deviations from the expected 1:1 ratio with a chi-square test (α=0.05).

Results

Size and age at maturity

Atlantic croaker mature at a small size and early age. Males and females started to mature at 170 and 150 mm, respectively; at lengths greater than these the percentages of mature fish increased rapidly (Fig. 2). Estimated mean length at first maturity (L_{50}) was 182 mm for males (SE=1.46 mm) and 173 mm for females (SE=1.33 mm). For both sexes, all individuals ≥250–260 mm were mature.

The percentage of mature fish by age showed a similar pattern of early maturation. More than 85% of both males and females were sexually mature by the end of their first year and all were mature by the end of their second.

Spawning

Spawning of Atlantic croaker in the Chesapeake Bay and adjacent coastal waters extends over a protracted period. Females in spawning phase (gonad stages: fully developed (3), gravid (4), or running-ripe (5); Table 1) were collected from July through December

(Fig. 3). However, the capture of developing females (stage 2) from May through August and regressing females (stage 6) from September through December indicates that spawning initiation and cessation were not synchronous among individuals. Although the population spawned over a six-month interval (July–December), individuals apparently spawned over a shorter period. Most females appeared to spawn for 3–4 months as indicated by the large percentages of fully developed (stage 3) ovaries from August through November.

The pattern of gonad development in males provided further evidence of an extended spawning season for Atlantic croaker. Mean and maximum GSI values increased sharply during July and August, and remained relatively high until November or December, depending on the year (Fig. 4). In addition, males with very large testes and free-running milt were common during August–September in collections from all locations and sampling gears, indicating intense male spawning during this period.

Spawning of Atlantic croaker occurred in the estuary as well as in coastal oceanic waters. Females with hydrated oocytes (gonad stages 4 and 5), indicative of imminent spawning, were collected in the lower York and James rivers (n=8 in 1990; n=3 in 1991; Fig. 3) and from coastal waters off Virginia and North Carolina (n=1 in 1990; n=3 in 1991; Fig. 3). Collections of spawning fish (gonad stages 3–5) in Chesapeake Bay during the period July–October (n=649 in 1990; n=277 in 1991; Fig. 3) and from offshore waters during November–December (n=39 in 1990; n=11 in 1991; Fig. 3) suggest spawning continues offshore and south as Atlantic croaker migrate from the estuary. However, the presence during September–October of regressing and resting females in Chesapeake Bay (n=39 in 1990; n=24 in 1991; Fig. 3) indicates that some individuals may complete their spawning in estuarine waters.

Although gravid and running-ripe females were collected during most of the spawning season (August–November, Fig. 3), they were present in very low numbers. During both years of sampling only seven gravid and eight running-ripe females were collected. In Chesapeake Bay, despite the large number of poundnet and haul-seine collections (1,422 mature females processed), gravid or running-ripe females were obtained only from gill nets and mainly from collections from the lower James River (six gravid and four running-ripe females). Daily gillnet collections in the lower York River during August–October 1990 and July–October 1991 (456 mature females processed) showed only one running-ripe and one partially spent female, i.e. a fully developed female that had fresh left-over hydrated oocytes in the ovarian lumen indicating recent spawning but that still had a large number of advanced yolked oocytes and could potentially spawn again. Offshore collections during November–December of 1990 and 1991

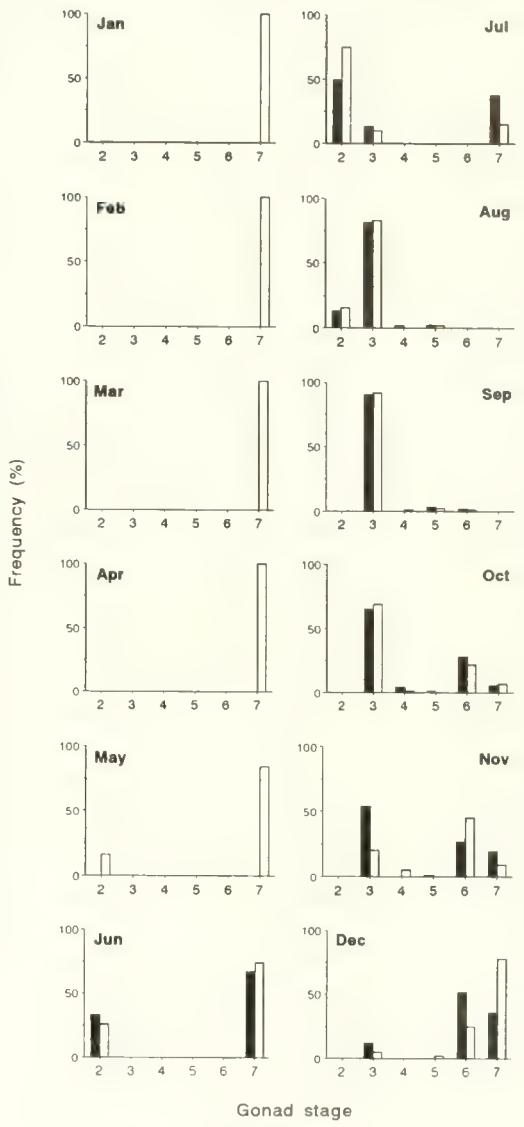

Figure 3

Percentage of gonad maturity stages by month for mature female Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters. Black bars=1990 data; open bars=1991 data. Gonad stages are (2) developing; (3) fully developed; (4) gravid; (5) running-ripe; (6) regressing; and (7) resting. Monthly sample sizes are presented in Table 2. Samples from April to October are from Chesapeake Bay; samples from November to March are from coastal waters off Virginia and North Carolina.

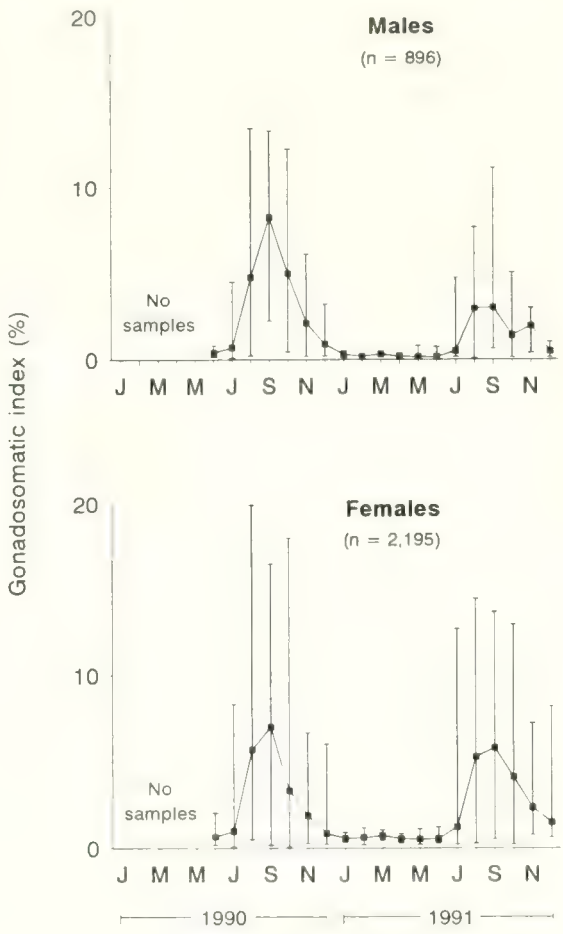

Figure 4

Monthly mean gonadosomatic index for male and female Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters, 1990–91. Vertical bars are ranges. *n*=sample size. Monthly sample sizes are presented in Table 2.

also showed a small percentage of gravid and running-ripe females (Fig. 3).

Sex ratios

Atlantic croaker showed wide temporal fluctuations in sex ratio. During both years, the frequency of males in samples decreased in June and July at the beginning of the spawning season, reached a minimum in the period of September–October, and increased again during November–December. Chi-square tests (Table 2) showed highly significant differences ($P<0.01$) in sex ratios between months over the periods July–October 1990 and June–October 1991.

Table 2

Number of males and females by month and chi-square tests for the monthly sex ratios of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters, 1990–91. **=$P<0.01$.

		Number of		
Year	Month	males	females	Chi-square
1990	Jun	107	71	3.64
	Jul	185	358	27.80**
	Aug	132	357	51.74**
	Sep	40	249	74.91**
	Oct	33	99	16.50**
	Nov	56	64	0.22
	Dec	41	33	0.37
1991	Jan	22	26	0.04
	Feb	27	27	—
	Mar	25	23	0.04
	Apr	36	51	1.29
	May	98	121	1.10
	Jun	52	129	15.96**
	Jul	44	103	11.84**
	Aug	21	122	34.96**
	Sep	16	119	38.99**
	Oct	9	75	25.61**
	Nov	15	33	3.37
	Dec	32	40	0.44

Oocyte development and spawning pattern

Monthly oocyte diameter distributions of fully developed females collected throughout the spawning season showed three main groups of oocytes (Fig. 5). However, oocyte development appears to be asynchronous; there is a large degree of overlap and no clearly defined limits between modal groups. Histological analysis showed that the first group, ranging approximately from 0.06 to 0.24 mm diameter, is composed mainly of primary growth and cortical alveolus oocytes but may include a few partially yolked oocytes in the beginning stages of yolk deposition (0.22–0.24 mm diameter). The second group, ranging approximately from 0.26 to 0.38 mm diameter, is composed of partially yolked oocytes in several stages of yolk deposition. The third group, ranging approximately from 0.40 to 0.60 mm diameter, is formed by advanced yolked oocytes and probably represents the group from which individual spawning batches will be formed.

Although frequency distributions of gonad stages and oocyte diameters (Figs. 3 and 5) indicated Atlantic croaker are multiple spawners with indeterminate fecundity, postovulatory follicles (POF's) were identified only in recently ovulated, running-ripe fe-

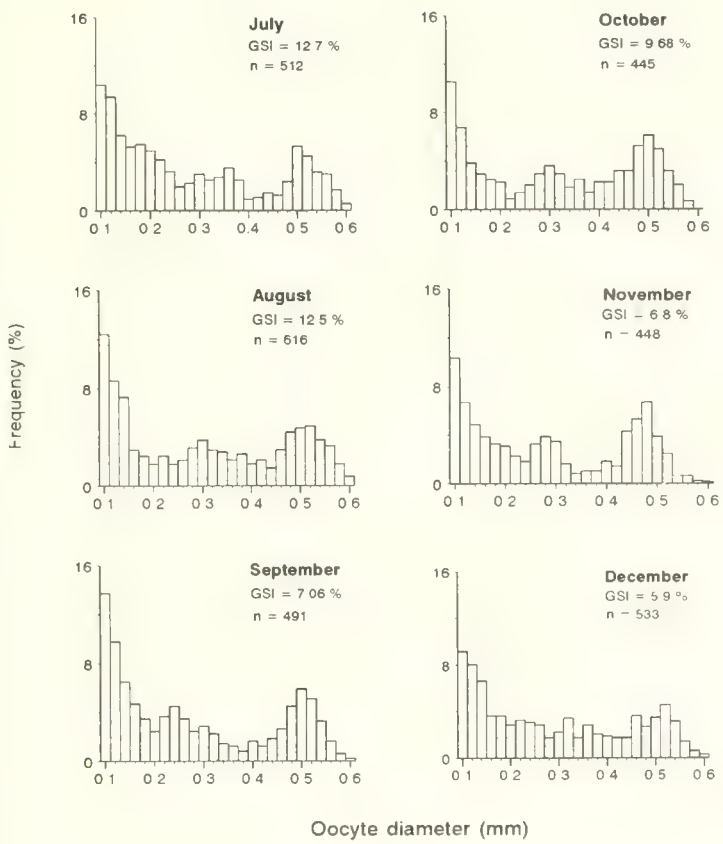

Figure 5

Monthly oocyte diameter distributions during the spawning season of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters. Each panel represents one female in the fully developed gonad stage. Samples from July to October are from Chesapeake Bay; samples from November to December are from coastal waters off Virginia and North Carolina. GSI=gonadosomatic index; *n*=number of oocytes measured.

males. No POF's were found in fully developed females, even those with left-over hydrated oocytes in the posterior end of the ovarian lumen. As a result, it was usually impossible to distinguish fully developed females spawning for the first time from those that had spawned at least once before (partially spent females).

Atresia of advanced yolked oocytes

Spawning-phase Atlantic croaker females (gonad stages 3–5; Table 1) showed a high incidence of α atresia of advanced yolked oocytes throughout the spawning season (July–December). However, the exact proportion of atretic oocytes could not be determined because of the difficulty in identifying oocytes in very early stages of atresia. Some females showed healthy advanced yolked oocytes, atretic advanced yolked oocytes in different stages of degeneration, and atretic follicles (β-, γ-, and δ-stage atresia) in the same ovary.

Compared with healthy oocytes (Fig. 6A), early phases of α atresia of advanced yolked oocytes in Atlantic croaker are characterized by the disintegration of the nucleus, which loses its integrity, becoming amorphous and slightly basophilic, and by the disintegration of yolk globules, which begin to dissolve, forming a continuous, amorphous mass, especially around the nucleus (Fig. 6B). At this stage, the majority of yolk granules at the periphery of the cytoplasm still maintain their structural integrity, spherical shape, and strong acidophilic staining. At intermediate stages, disintegration of yolk globules progresses towards the peripheral cytoplasm, which by now may have a band of dark, basophilic material (Fig. 6C), and the zona radiata begins to deteriorate. At late stages of α atresia (Fig. 6D), the nucleus has completely disappeared, the zona radiata has lost its structural integrity, and the cytoplasm has been invaded by phagocytizing granulosa cells. Only portions of dissolved yolk and a few yolk globules remain at this stage. However, atresia will continue until the oocyte is completely resorbed, leaving only the remaining follicle. After this phase, α-stage atresia has been completed and follicular atresia begins with the resorption of the remaining granulosa and thecal cells.

Comparisons of fresh oocyte samples with histology slides confirmed the high incidence of α atresia of advanced yolked oocytes in Atlantic croaker. Although the histological method appeared more sensitive in detecting earlier stages of atresia (Fig. 7A), the use of fresh oocytes was indispensable. Fresh oocytes provided an easy, fast way to assess gonad condition and to identify oocyte atresia. A large proportion of atretic advanced yolked oocytes could be easily identified by clumping and darkening of the yolk granules, formation of a clear zone in the peripheral cytoplasm (Fig. 7B), and at later stages, formation of several light yellow vacuoles (Fig. 7C).

Description of the ovarian cycle

A diagrammatic representation of the Atlantic croaker ovarian cycle, based on the temporal distri-

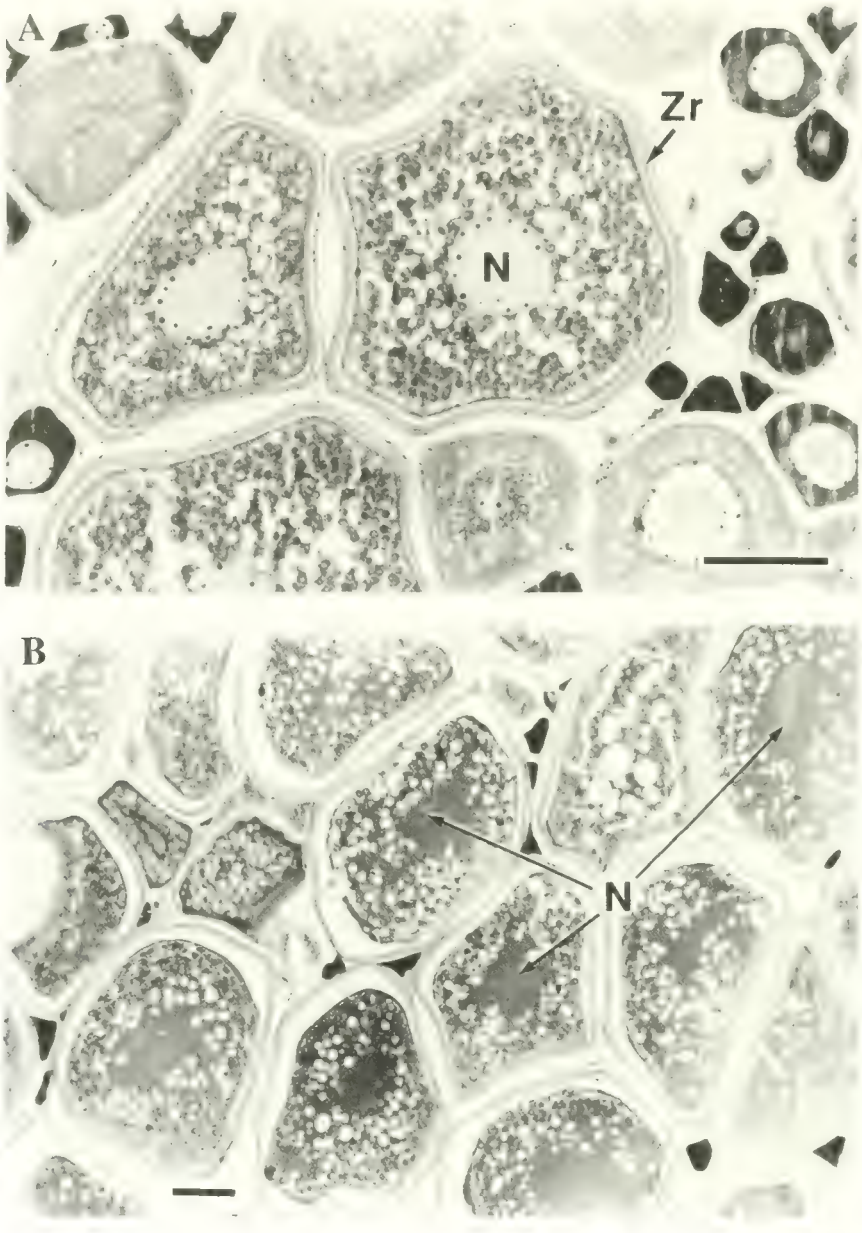

Figure 6

Appearance of advanced yolked oocytes of Atlantic croaker, *Micropogonias undulatus*. (**A**) healthy (nonatretic) oocyte; (**B**) oocytes in early stage of α atresia; (**C**) oocyte in intermediate stage of α atresia; (**D**) oocytes in late stage of α atresia. N=nucleus; Zr=zona radiata; Pc=peripheral cytoplasm; La=late stage of α atresia. Bars=0.1 mm.

bution of maturity stages and the pattern of oocyte development is presented in Figure 8. The cycle can start either with immature females, which enter the cycle for the first time by reaching sexual maturity, or with adult resting females, which restart the cycle by entering the developing stage at the beginning of each spawning season. After the first batch of advanced yolked oocytes is completed, females, now in the fully developed stage, go through a smaller cycle (spawning phase) that characterizes the pattern of multiple spawning and indeterminate fecundity of Atlantic croaker. During this phase, fully developed

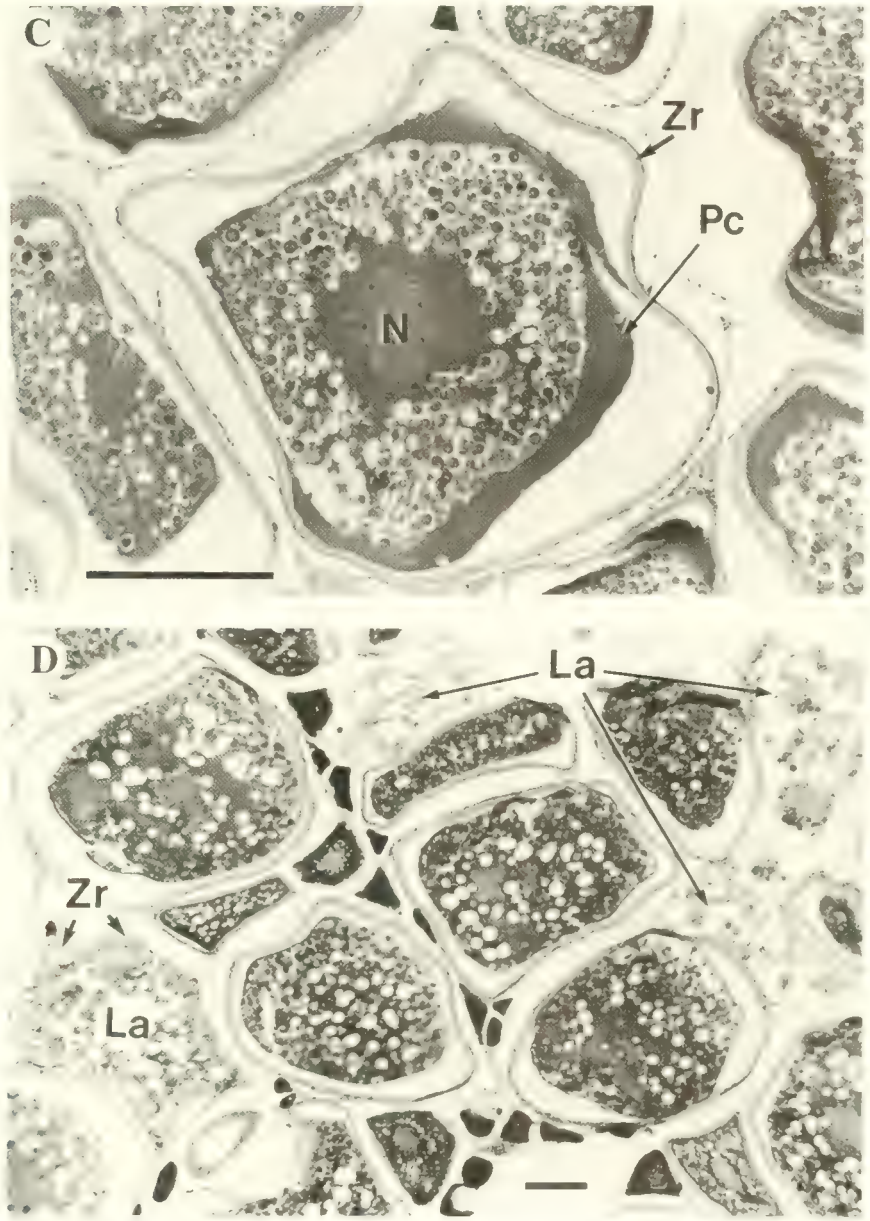

Figure 6 (Continued)

females cycle through the gravid and running-ripe stages by undergoing the processes of hydration, ovulation, and spawning. If spawning has not been completed, left-over advanced yolked oocytes are resorbed, a new batch of advanced yolked oocytes is recruited from the group of partially yolked oocytes (redeveloping process), and females are ready to go through the cycle again. If spawning is completed, females will then move to the regressing stage, where, through the process of oocyte atresia, left-over oocytes (cortical alveoli to advanced yolked stage) will be resorbed, after which ovaries return to the resting stage.

Discussion

Spawning periodicity

Our results on spawning periodicity of Atlantic croaker agree with previous reports for the Chesapeake Bay and mid-Atlantic regions. Prior studies

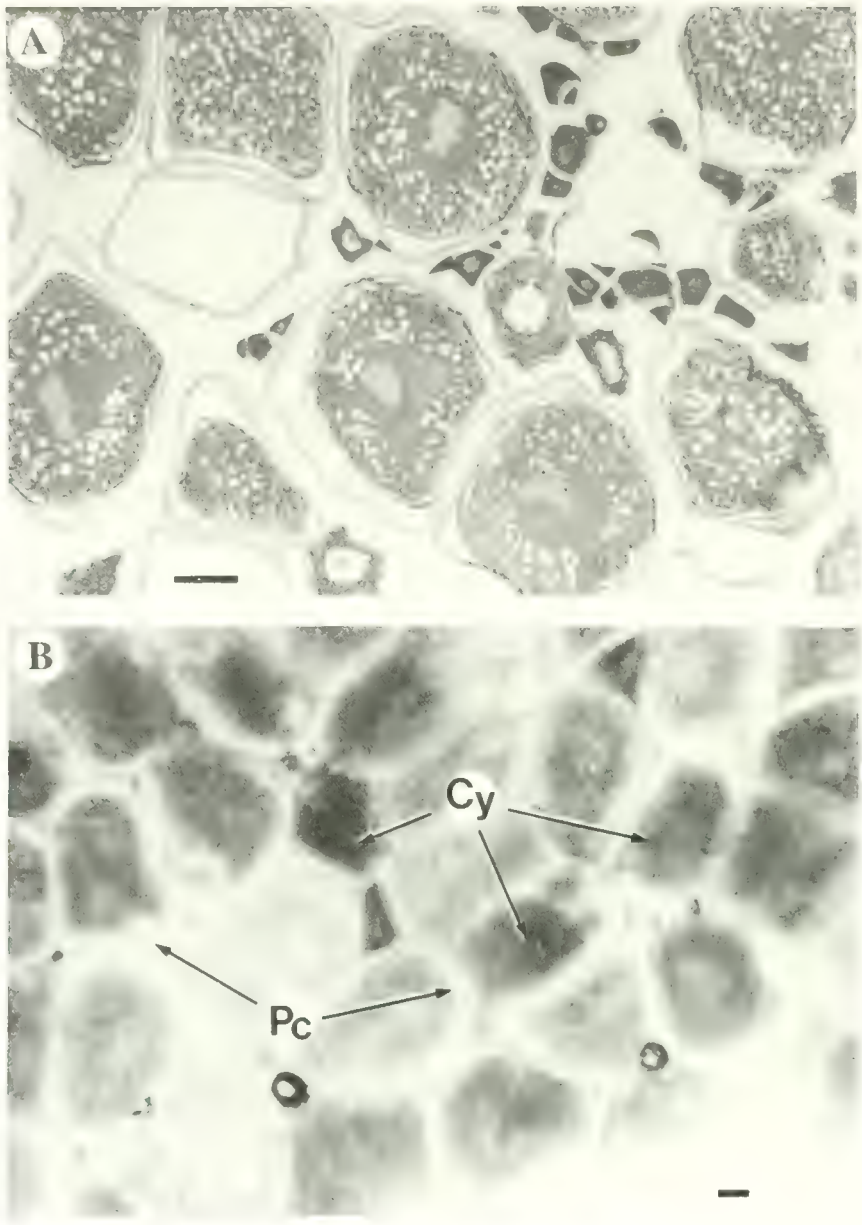

Figure 7

Comparison of the appearance of α-atretic advanced yolked oocytes of a fully developed Atlantic croaker, *Micropogonias undulatus*, in a histology slide (**A**), and in a smear of fresh oocytes under a dissecting scope (**B**) and (**C**). Cy=clumping of yolk globules; Pc=peripheral cytoplasm; Va=vacuoles. Bars=0.1 mm.

(Welsh and Breder, 1923; Wallace, 1940; Johnson, 1978; Colton et al., 1979; Morse, 1980) describe a protracted spawning season, extending from July/August through November/December, with peak spawning during September/October. However, reports of spawning from September/October through March/April along the South Atlantic Bight (Hildebrand and Cable, 1930; Bearden, 1964; Warlen, 1982; Lewis and Judy, 1983) indicate that south of Cape Hatteras, North Carolina, spawning seems to start a little later and to continue through early spring, perhaps as a result of the southward late summer/early fall migration of Atlantic croaker (Hildebrand and Schroeder, 1928; Wallace, 1940; Haven, 1959).

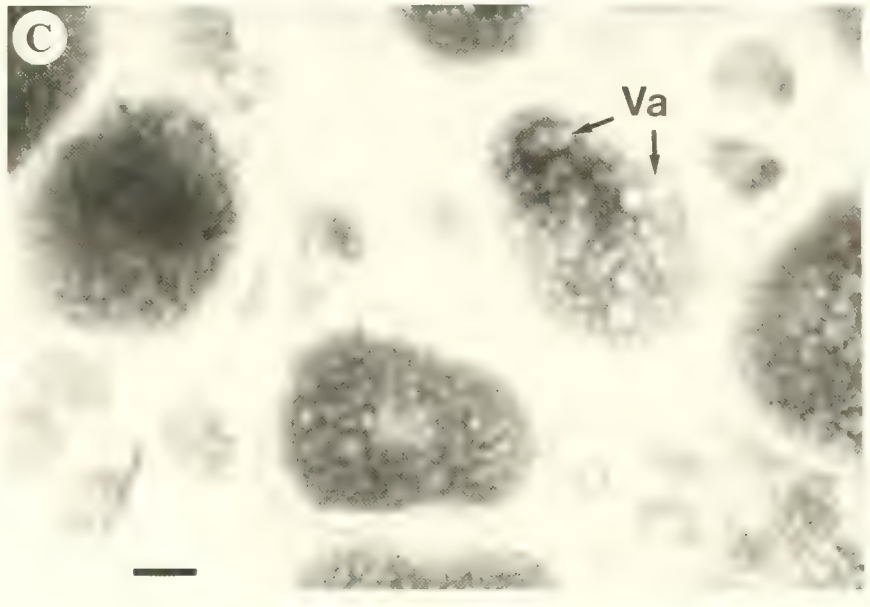

Figure 7 (Continued)

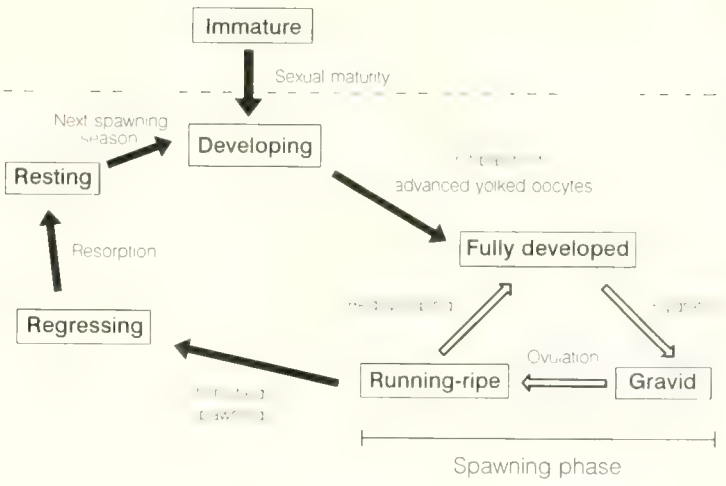

Figure 8

Diagrammatic representation of the ovarian cycle of Atlantic croaker, *Micropogonias undulatus* (see text for details).

The presence of small juveniles (<20 mm TL) in the York River from August/September through May/June has prompted suggestions that north of Cape Hatteras spawning of Atlantic croaker may also continue through spring (Haven, 1957; Chao and Musick, 1977). However, our results confirm previous reports (Wallace, 1940; Colton et al., 1979; Morse, 1980) that in the Chesapeake Bay and mid-Atlantic regions spawning is essentially completed by the end of December.

Although Welsh and Breder (1923) suggested that spawning might take place in large estuaries such as the Delaware and Chesapeake bays, this study represents the first documented report of estuarine spawning for Atlantic croaker. Previous studies have consistently described Atlantic croaker as strict marine spawners whose larval and juvenile stages migrate into estuarine nursery areas (Pearson, 1929; Hildebrand and Cable, 1930; Wallace, 1940; Haven,

1957; Warlen, 1982; Lewis and Judy, 1983; Setzler-Hamilton, 1987). However, the fact that during both years we found spawning-phase females (stages 3–5) in Chesapeake Bay from July through October and that regressing and resting females—which probably had completed spawning for the season—were collected in the estuary indicates that the role of estuaries as additional spawning areas for Atlantic croaker may be more important than previously thought. Other sciaenids that were believed to be strict marine spawners have also been reported to spawn occasionally in estuaries (Castello, 1985; Johnson and Funicelli, 1991). However, whether significant spawning of Atlantic croaker occurs in Chesapeake Bay or other estuaries requires further investigation.

The fact that spawning-phase Atlantic croaker have not previously been found in Chesapeake Bay can be attributed, at least in part, to their pattern of multiple spawning and indeterminate fecundity. Because in multiple spawning fishes the processes of hydration, ovulation, and spawning usually occur within a matter of hours (Hunter and Macewicz, 1985a; Brown-Peterson et al., 1988), the probability of collecting gravid or running-ripe females is much lower compared with other maturity stages. Additionally, contrary to what happens with total spawners, partially spent ovaries contain oocytes ranging from primary growth to advanced yolked stage, making the macroscopic identification of post-spawning fish very difficult (Hunter and Macewicz, 1985a). In most cases, we were not able to distinguish macroscopically between fully developed and partially spent ovaries, and this also may have been a problem with previous studies (e.g. Wallace, 1940).

Diel periodicity of spawning could also influence the occurrence of hydrated females in samples from different gears. The thousands of adult Atlantic croaker examined by Haven (1957) and Wallace (1940) were collected primarily from Chesapeake Bay commercial pound nets and haul seines, which are usually fished in the predawn or early morning hours (Reid, 1955; Chittenden, 1991). During the rest of the day and through most of the night, fish remain alive in the pound-head or in the seine-bag until the nets can be fished (emptied), usually during slack water, and between 4:00 and 9:00 am. We hypothesize that during this period Atlantic croaker spawn within the nets at their usual spawning time of dusk (Holt et al., 1985). Females collected from these nets the following morning would probably show little or no signs of spawning and be identified as "developing" (Wallace, 1940) or fully developed (this study). However, contrary to what happens with pound nets and haul seines, gill nets usually kill the fish within a short time after capture. Females undergoing hydration or ovulation, especially those caught a few hours before dusk, would die before they finished spawning, and the presence of hydrated oocytes in the ovaries could be recorded. This may explain why we observed hydrated or recently spent females only in gillnet collections. A similar pattern has also been observed for weakfish, *Cynoscion regalis*, which, like Atlantic croaker, spawn primarily between 6:00 and 9:00 pm.[1]

Size and age at maturity

Our estimates of size and age at maturity are generally below values previously reported for Atlantic croaker in the Chesapeake Bay and mid-Atlantic regions. Disagreement with previous reports can be attributed to three main factors: 1) failure of at least some studies (Wallace, 1940; Morse, 1980) to sample small, young fish from fishery-independent sampling programs; 2) the inclusion of samples collected from a period when resting (reproductively inactive) fish were present in the estimation of the proportion of mature fish by size or age; and 3) disagreement with previous estimates of age at maturity probably reflects problems with age-determination methods previously used for Atlantic croaker. Because of the difficulty in distinguishing resting and immature gonads, estimates based on samples pooled over the entire spawning season or during a period when resting fish were present (e.g. Wallace, 1940; Morse, 1980) are probably biased towards larger sizes or older ages. Hunter et al. (1992) found that estimates of L_{50} for Dover sole were higher when females were taken during the spawning season than when they were sampled before spawning began. They suggested that estimates of length or age at first maturity should always be based on samples collected prior to the onset of spawning, when postspawning females with highly regressed ovaries are rare. However, for species like Atlantic croaker, which show individually asynchronous gonadal maturation, sampling before the onset of spawning will not prevent the occurrence of prespawning, resting fish. To avoid this problem we used only fish collected in September, when no resting or developing stages occurred, to estimate size and age at first maturity. Finally, disagreement with previous estimates of age at maturity probably reflects problems with age-determination methods previously used for Atlantic croaker. The use of length frequencies (Welsh and Breder,

[1] Lowerre-Barbieri, S. K., M. E. Chittenden Jr., and L. R. Barbieri. 1993. The multiple spawning pattern of weakfish, *Cynoscion regalis*, in the Chesapeake Bay and mid-Atlantic Bight, with a discussion of annual fluctuations in reproductive output. Virginia Institute of Marine Science, Gloucester Point, VA 23062. Unpubl. manuscr., 61 p.

1923) requires considerable subjective interpretation given the extended spawning season of Atlantic croaker, the generally asymptotic growth after age 2, and the great overlap in observed sizes at age (Barbieri et al., 1994). Although Welsh and Breder (1923) and Wallace (1940) have also used scales, problems in applying this method to Atlantic croaker have been reported (Joseph, 1972).

Sex ratios

Our results on temporal fluctuations in Atlantic croaker sex ratios agree well with previous reports for the Chesapeake Bay and mid-Atlantic regions (Welsh and Breder, 1923; Wallace, 1940). The predominance of females during the first 3–4 months of spawning may indicate that either males start leaving the estuary earlier than females as fish migrate out of Chesapeake Bay or that spawning-phase females are more susceptible to the fishing gears used in Chesapeake Bay (pound nets, haul seines, and gill nets). During both years, the frequency of males decreased during the first two months of spawning and began increasing again in October/November when the first offshore trawl collections were obtained. Mark-recapture studies are necessary to better evaluate the migratory patterns of Atlantic croaker in Chesapeake Bay and the mid-Atlantic region.

Atresia of advanced yolked oocytes

High levels of atresia typically have been used to identify regressing ovaries, and for many teleosts, have been described as representing a key histological marker for the cessation of spawning (Hunter and Macewicz, 1985, a and b; Hunter et al., 1986; Dickerson et al., 1992). However, our results with Atlantic croaker indicate that high levels of atresia do not necessarily imply the end of spawning. Although we found significant atresia of cortical alveoli and partially yolked oocytes only in regressing ovaries, indicating it could in fact be used to mark the end of spawning, major atresia of advanced yolked oocytes was observed in actively spawning females throughout the spawning season suggesting it may represent a normal part of the reproductive biology of Atlantic croaker. The fact that hydrated females—either actively spawning or just about to spawn—showed advanced yolked oocytes undergoing atresia suggests that a portion of these oocytes are never matured and spawned. In other words, it appears that a surplus production of advanced yolked oocytes is part of the reproductive strategy of Atlantic croaker. Fully developed females may hydrate and spawn more or less of these oocytes depending, for example, on environmental conditions.

Evidence from laboratory studies seems to support this hypothesis. Middaugh and Yoakum (1974) used chorionic gonadotropin to induce laboratory spawning of Atlantic croaker. They found that although the abdomen of females became extremely distended as a result of oocyte hydration, only a limited number of eggs could be stripped from each fish. More recently, Trant and Thomas (1988) and Patiño and Thomas (1990) evaluated in vitro germinal vesicle breakdown (GVBD, an index of final oocyte maturation) in laboratory-spawned Atlantic croaker. They reported that in this species there is always a residual number of "advanced oocytes" which fail to complete GVBD or even enter the morphological maturation process, suggesting that not all oocytes in a spawning batch would be matured and spawned.

Conclusion

Because of the small number of gravid females collected and the fact that POF's could be identified only in running-ripe females, we were not able to estimate batch fecundity and spawning frequency for Atlantic croaker. However, our results have shown that 1) Atlantic croaker mature at a smaller size and earlier age than previously thought; 2) Atlantic croaker are capable of spawning in the estuary, although the magnitude of estuarine spawning is still unclear; 3) they are multiple spawners with indeterminate fecundity, indicating that the only available estimates of fecundity (Morse, 1980)—those based on the assumption of determinate fecundity—should not be used for management; and 4) the oocyte size-frequency method (MacGregor, 1957) should not be used to estimate batch fecundity for this species, because of the high levels of atresia of advanced yolked oocytes observed in spawning females. Future studies on the reproductive biology of Atlantic croaker in Chesapeake Bay and the mid-Atlantic region should concentrate on offshore, preferably fishery-independent, trawl collections to obtain gravid females for batch fecundity estimates following the hydrated oocyte method (Hunter et al., 1985). Rates of deterioration and resorption of POF's must also be evaluated in laboratory-spawned fish to determine if the postovulatory follicle method (Hunter and Macewicz, 1985a) can be used to estimate spawning frequency for this species.

Acknowledgments

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Literature cited

Barbieri, L. R., M. E. Chittenden Jr., and C. M. Jones.
1994. Age, growth, and mortality of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay region, with a discussion of apparent geographic changes in population dynamics. Fish. Bull. 92:1–12.

Brown-Peterson, N., P. Thomas, and C. R. Arnold.
1988. Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in south Texas. Fish. Bull. 86:373–388.

Bearden, C. M.
1964. Distribution and abundance of Atlantic croaker, *Micropogon undulatus*, in South Carolina. Contrib. Bears Bluff Lab., South Carolina 40:1–23.

Castello, J. P.
1985. The ecology of consumers from dos Patos Lagoon estuary, Brazil. *In* A. Yáñez-Arancibia (ed.), Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration, chapter 17, p. 383–406. DR(R) UNAM Press, Mexico.

Chao, L. N., and J. A. Musick.
1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull. 75:657–702.

Chittenden, M. E., Jr.
1991. Operational procedures and sampling in the Chesapeake Bay pound-net fishery. Fisheries (Bethesda) 16:22–27.

Colton, J. B., Jr., W. G. Smith, A. W. Kendall Jr., P. L. Berrien, and M. P. Fahay.
1979. Principal spawning areas and times of marine fishes, Cape Sable to Cape Hatteras. Fish. Bull. 76:911–915.

DeMartini, E. E., and R. K. Fountain.
1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull. 79:547–560.

Dickerson, T. L., B. J. Macewicz, and J. R. Hunter.
1992. Spawning frequency and batch fecundity of chub mackerel, *Scomber japonicus*, during 1985. Calif. Coop. Oceanic Fish. Invest. Rep. 33:130–140.

Haven, D. S.
1957. Distribution, growth, and availability of juvenile croaker, *Micropogon undulatus*, in Virginia. Ecology 38:88–97.
1959. Migration of the croaker, *Micropogon undulatus*. Copeia 1959:25–30.

Hildebrand, S. F., and W. C. Schroeder.
1928. The fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43:1–388.

Hildebrand, S. F., and L. E. Cable.
1930. Development and life history of fourteen teleostean fishes at Beaufort, N.C. Bull. U.S. Bur. Fish. 46:383–488.

Holt, G. J., S. A. Holt, and C. R. Arnold.
1985. Diel periodicity of spawning in sciaenids. Mar. Ecol. Prog. Ser. 27:1–7.

Horwood, J. W., and M. Greer Walker.
1990. Determinacy of fecundity in sole (*Solea*) from the Bristol Channel. J. Mar. Biol. Assoc. U.K. 70:803–813.

Hunter, J. R., and S. R. Goldberg.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull. 77:641–652.

Hunter, J. R., and B. J. Macewicz.
1985a. Measurement of spawning frequency in multiple spawning fishes. *In* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, p. 79–94. Dep. Commer., NOAA Tech. Rep. NMFS 36.
1985b. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish. Bull. 83:119–136.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong.
1985. Batch fecundity in multiple spawning fishes. *In* R. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fishes: application to the northern anchovy, *Engraulis mordax*, p. 67–77. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Hunter, J. R., B. J. Macewicz, and J. R. Sibert.
1986. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific. Fish. Bull. 84:895–903.

Hunter, J. R., B. J. Macewicz, N. C. H. Lo, and C. A. Kimbrell.
1992. Fecundity, spawning, and maturity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull. 90:101–128.

Johnson, G. D.
1978. *Micropogonias undulatus* (Linnaeus), Atlantic croaker. Dep. Interior, U.S. Fish and Wildl. Serv. FWS/OBS-78/12:227–233.

Johnson, D. R., and N. A. Funicelli.
1991. Spawning of the red drum in Mosquito Lagoon, east-central Florida. Estuaries 14:74–79.

Joseph, E. B.
1972. The status of the sciaenid stocks of the middle Atlantic coast. Chesapeake Sci. 13:87–100.

Lewis, R. M., and M. H. Judy.
1983. The occurrence of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in Onslow Bay and Newport River estuary, North Carolina. Fish. Bull. 81:405–412.

Lowerre-Barbieri, S. K., and L. R. Barbieri.
1993. A new method of oocyte separation and preservation for fish reproduction studies. Fish. Bull. 91:167–170.

Macer, C. T.
1974. The reproductive biology of horsemackerel, *Trachurus trachurus* (L.), in the North Sea and English Channel. J. Fish Biol. 6:415–438.

MacGregor, J. S.
1957. Fecundity of the Pacific sardine (*Sardinops caerulea*). Fish. Bull. 57:427–449.

McHugh, J. L.
1981. Marine fisheries of Delaware. Fish. Bull. 79:575–599.

Middaugh, D. P., and R. L. Yoakum.
1974. The use of chorionic gonadotropin to induce laboratory spawning of the Atlantic croaker, *Micropogonias undulatus*, with notes on subsequent embryonic development. Chesapeake Sci. 15:110–114.

Morse, W. W.
1980. Maturity, spawning and fecundity of Atlantic croaker, *Micropogonias undulatus*, occurring north of Cape Hatteras, North Carolina. Fish. Bull. 78:190–195.

Norcross, B. L., and H. M. Austin.
1988. Middle Atlantic Bight meridional wind component effect on bottom water temperatures and spawning distribution of Atlantic croaker. Cont. Shelf Res. 8:69–88.

Patiño, R., and P. Thomas.
1990. Induction of maturation of Atlantic croaker oocytes by 17α, 20β, 21-trihydroxy–4-pregnen–3-one in vitro: consideration of some biological and experimental variables. J. Exp. Zool. 255:97–109.

Pearson, J. C.
1929. Natural history and conservation of the redfish and other commercial sciaenids on the Texas coast. Bull. Bur. Fish. 44:129–214.
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the grey seatrout *Cynoscion regalis* (Bloch). Bull. U.S. Fish. Wildl. Serv. 50:79–102.

Reid, G. K., Jr.
1955. The pound-net fishery in Virginia. Part 1: History, gear description, and catch. Comm. Fish. Rev. 17(5):1–15.

Saila, S. B., C. W. Recksieck, and M. H. Prager.
1988. Basic fisheries science programs. Elsevier, New York, 230 p.

Setzler-Hamilton, E. M.
1987. Utilization of Chesapeake Bay by early life history stages of fishes. *In* S. K. Majumdar, L. W. Hall, and H. M. Austin (eds.), Contaminant problems and management of living Chesapeake Bay resources, p. 63–93. The Pennsylvania Academy of Science, Philadelphia, Pennsylvania.

Trant, J. M., and P. Thomas.
1988. Structure-activity relationships of steroids in inducing germinal vesicle breakdown of Atlantic croaker oocytes in vitro. Gen. Comp. Endocrinol. 71:307–317.

Wallace, D. H.
1940. Sexual development of the croaker, *Micropogon undulatus*, and distribution of the early stages in Chesapeake Bay. Trans. Am. Fish. Soc. 70:475–482.

Wallace, R. A., and K. Selman.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

Warlen, S. M.
1982. Age and growth of larvae and spawning time of Atlantic croaker in North Carolina. Proc. Annu. Conf., S.E. Assoc. Fish Wildl. Agencies 34:204–214.

Welsh, W. W., and C. M. Breder.
1923. Contributions to life histories of Sciaenidae of the eastern United States coast. Bull. U.S. Bur. Fish. 39:141–201.

Biochemical and histological changes during ovarian development of cobia, *Rachycentron canadum*, from the northern Gulf of Mexico

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Abstract.—Female cobia, *Rachycentron canadum*, were sampled on their spawning grounds in the northern Gulf of Mexico to study changes in proximate analysis (protein, lipid, carbohydrate, and ash) of the ovaries during gonadal maturation. Four major stages of oocyte development were studied: stage 1, previtellogenesis; stage 2, vitellogenesis; stage 3, final maturation; and stage 4, postovulation. Cobia are multiple spawning fish; therefore, ovaries engaged in a sequential round of oogenesis were distinguished as stages 1' and 2'. Protein was the major constituent of cobia ovaries and its contribution remained fairly constant (49–55% of the dry weight) throughout all stages of development. Lipid was the second most abundant component but the levels, ranging from 21 to 41%, changed depending on the stage of ovarian development. Lipid concentration increased from stage 1 through 3 and decreased slightly in stage 4; it was lower in stage-1 than in stage-1' ovaries but was the same in stages 2 and 2'. Carbohydrate was the least abundant component (3–4%) whereas ash ranked third (6–20%). Most cobia were in prespawning condition (stages 1–3) when they arrived in the northern Gulf of Mexico in April and May; some prespawning fish (stages 1 and 2) were also observed in August and September about a month or two before migration to the overwintering grounds normally occurs. Cobia undergoing sequential spawning episodes (stages 1' and 2') were captured from April through August. Gonosomatic indices (GSI) were calculated both for ovarian developmental stage and for month of capture. Mean GSI increased as ovarian development proceeded and decreased during postovulation; GSI for month of capture was highest during April and May when the prespawning fish first appeared in northern Gulf of Mexico waters.

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Cobia, *Rachycentron canadum*, are large migratory fish with a worldwide distribution in tropical and subtropical seas, except for the Pacific coast of North America (Migdalski and Fichter, 1983). In the western Atlantic, cobia are found from Massachusetts and Bermuda to Argentina (Briggs, 1958) but are most common in the Gulf of Mexico (Migdalski and Fichter, 1983), ranging from Key West along the entire coast to Campeche, Mexico (Dawson, 1971). Cobia support a popular sport fishery wherever they are present. Total mortality rates for cobia, including sport and commercial catches plus natural mortality, may be high (Richards, 1967) and it has been questioned whether cobia in the Gulf of Mexico are being exploited at rates beyond which maximum sustainable yields can be maintained.

Cobia undergo extensive seasonal migrations (Fig. 1), moving from overwintering grounds to distant spawning/feeding grounds during the spring and summer (Briggs, 1958). They are usually absent from the U.S. fishery in more northerly latitudes during fall and winter months (Dawson, 1971) and are believed to spend their winters near the Florida Keys.[1] During the spring, cobia move northwest into Gulf waters[1] or north along the eastern seaboard of the United States (Richards, 1977). Cobia usually enter north-central Gulf waters (Alabama and Mississippi) in March or April and begin the return to their wintering grounds in late September.[1]

Female cobia with ripe ovaries have been collected in the northern Gulf of Mexico from April to May through October.[2] Spawning takes place throughout the summer with

[1] Franks, J. S., J. T. McBee, and M. T. Allen. 1992. Studies on the seasonal movements and migratory patterns of the cobia, *Rachycentron canadum*, in Mississippi marine waters and adjacent Gulf waters. Gulf Coast Res. Lab., Ocean Springs, MS 39566-7000. Interim Contract Rep. to Miss. Dept. Wildl., Fish. and Parks/Bur. Mar. Res. and U.S. Fish Wildl. Serv., Atlanta, GA 30303, Project No. F-91, 62 p.

[2] Lotz, J. M., R. M. Overstreet, and J. S. Franks. 1991. Reproduction of cobia, *Rachycentron canadum*, from the northeastern Gulf of Mexico. *In* J. S. Franks, T. D. McIlwain, R. M. Overstreet, J. T. McBee, J. M. Lotz, and G. Meyer, Investigations of the cobia (*Rachycentron canadum*) in Mississippi marine waters and adjacent Gulf waters. Gulf Coast Res. Lab., Ocean Springs, MS 39564-7000. Final Rep. to Miss. Dept. Wildl., Fish. and Parks/Bur. Mar. Res. and U.S. Fish Wildl. Serv., Atlanta, GA 30303, Project No. F-91, p. 2-1 to 2-42.

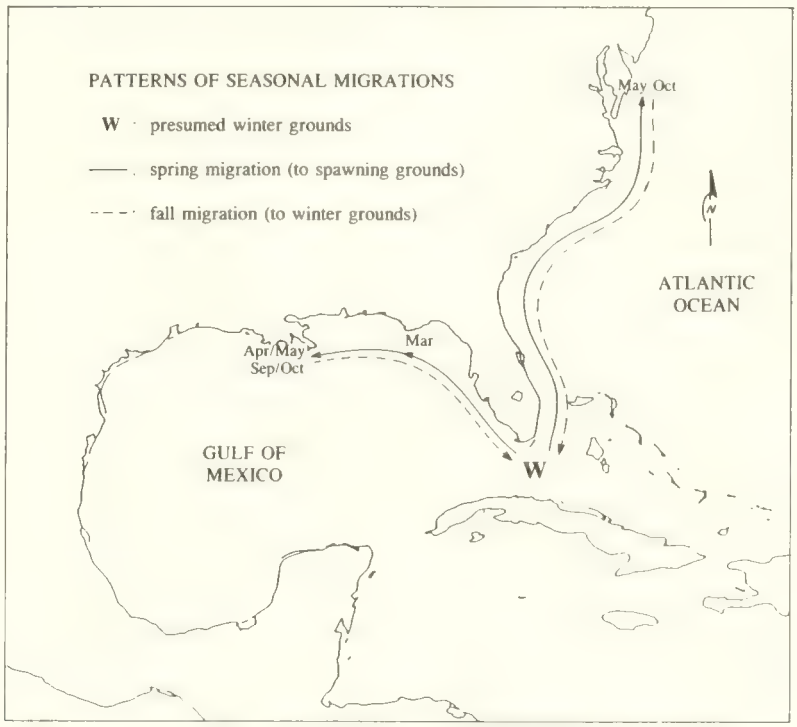

Figure 1

Patterns of seasonal migration of cobia, *Rachycentron canadum*, in the eastern Gulf of Mexico and U.S. Atlantic waters. Cobia are found west of the Mississippi River delta but little is known of their migratory patterns there (see Footnote 1 in text). Lines and arrows indicate presumed patterns of migration, not specific migratory routes.

mature females releasing eggs at least once but possibly twice or more during the breeding season; the population experiences a spawning peak during late spring or early summer. Fertilized cobia eggs are pelagic and egg diameter is between 1.16 and 1.42 mm (Joseph et al., 1964).

Although histological changes during development of cobia ovaries have been described previously,[2] nothing is known about biochemical changes in the ovary that occur during gonadal maturation. Data on the patterns of change in protein, lipid, and carbohydrate during oocyte development, and on the subsequent utilization of these reserves by the embryos and larvae are important to understanding the early life history of cobia. There is, in fact, very little information about interactions among these three nutrient reserves relative to reproduction despite intensive work on the nutritional requirements of a wide range of fish species.

Few studies have considered the relationship of the major biochemical components (protein, lipid, carbohydrate, and ash) throughout the course of fish ovarian development. Dawson and Grimm (1980) showed that protein was higher and more constant than lipid during gonadal development of plaice, *Pleuronectes platessa*; ash was low and carbohydrate was not measured. Other authors have studied only the ripe (prespawning) stage of fish ovaries. Ripe mullet, *Mugil cephalus* (Lu et al., 1979), and Atlantic cod, *Gadus morhua* (Kjesbu et al. 1991), ovaries also had higher protein than lipid levels and had low ash and carbohydrate. On the other hand, lipid was the major component of ripe anabantid *Trichogaster pectoralis* ovaries (Hails, 1983).

The present study addresses changes in biochemical composition of the cobia ovary throughout the course of gonadal development. Total protein, lipid, carbohydrate, and ash were measured and compared among fish sampled on their spawning grounds in the northern Gulf of Mexico; the different stages of gonadal development were confirmed histologically. In addition, gonosomatic indices (GSI) were calculated on the basis of ovarian developmental stage and month of capture.

Table 1

Stages of ovarian development in cobia, *Rachycentron canadum*.

Stage	Characteristics
1 Previtellogenesis	Germinal vesicle develops; evaginations appear in nuclear envelope; cortical alveoli form in ooplasm.
2 Vitellogenesis	Lipid vacuoles form; uneven dispersal of protein and lipid yolk.
3 Final maturation	Clearing of lipid around periphery of oocytes; enlarged size; chromosomes condense.
4 Postovulation	Oocytes become distorted and compacted; presence of postovulatory follicles; frothy residual lipid vacuoles.
1' Sequential previtellogenesis	Sequential development of previtellogenic oocytes after a spawning episode; presence of postovulatory follicles and resorbing oocytes in addition to characteristics of stage 1.
2' Sequential vitellogenesis	Sequential development of vitellogenic oocytes after a spawning episode; presence of postovulatory follicles and resorbing oocytes in addition to characteristics of stage 2.

Materials and methods

Sample collection

Cobia examined in this study were collected from coastal waters of Florida, Alabama, Mississippi, Louisiana, and Texas, mostly through fishing tournaments held along the northern Gulf Coast during April through September of 1991 and 1992, although a few fish were caught by project personnel during that same time period. Fish were stored on ice from the time of capture. Immediately after each fish was weighed and measured (total and fork lengths), the ovaries were removed, placed in plastic resealable bags, and stored on ice for 4 to 20 hours until gonad total weights could be recorded and aliquots of the tissue taken. Separate aliquots of each ovary sample were placed in 10% phosphate-buffered formalin and stored at room temperature until the tissues were processed for microscopic examination (see below). Additional aliquots of each ovary were stored at –80°C until the biochemical analyses (see below) were performed.

Histology

Ovaries were processed according to techniques modified from Humason (1979). Tissues were dehydrated in ethyl alcohol and embedded in paraffin by means of a Histomatic automatic tissue processor. The embedded tissues were sectioned at 4 or 5 µm. Sections were stained with Delafield's hematoxylin and eosin (95% ethyl alcohol) (Humason, 1979).

Aspects of fish ovarian development as described by Blaxter (1969), Wallace and Selman (1981), Overstreet (1983, a and b), Guraya (1986), and Mommsen and Walsh (1988) were used to determine the stages of development in cobia ovaries. Four categories of development were observed in this study: stage 1, previtellogenesis; stage 2, vitellogenesis; stage 3, final maturation, and stage 4, postovulation (Table 1). Some ovaries appeared to have entered another, sequential round of oocyte maturation. Because we were interested in biochemical differences that might exist between successive clutches of oocytes, the following additional categories were studied: stage 1', a sequential previtellogenesis, and stage 2', second (or sequential) vitellogenesis.

Biochemistry

The frozen tissues were thawed on ice and homogenized with either a Virtis tissue homogenizer or a hand-held ground glass mortar and pestle. Protein was measured according to Hartree (1972) with bovine serum albumin as the standard. Carbohydrate was measured according to Dubois et al. (1956) with glucose as the standard. Dry weight was determined after drying the samples overnight at 80°C to constant weight. The same samples were then combusted overnight at 500°C to determine ash content. Lipid extraction was performed according to Sasaki and Capuzzo (1984) which is a modification of Folch et al. (1957) and Bligh and Dyer (1959); total lipid was measured gravimetrically with a Cahn C-31 microbalance.

Calculations and statistics

A gonosomatic index (GSI) was calculated as

$$\text{GSI} = \text{ovary weight}/(\text{total fish weight} - \text{ovary weight}) \times 100$$

(DeVlaming et al., 1982).

Nonparametric Kruskal-Wallis analysis of variance by ranks (Zar, 1984) was performed with the SPSS-X2.1 statistical software package in order to test the null hypothesis that there were no significant differences among the means being compared. In cases

where the null hypothesis was rejected ($\alpha<0.05$), nonparametric Tukey-type multiple comparisons were performed according to Zar (1984) in order to determine between which of the mean values significant differences occurred.

Results

Histology

Histological analyses were performed on the gonads of 115 female cobia collected from the northern Gulf of Mexico over the course of two breeding seasons (n=42 in 1991 and n=73 in 1992). Of these fish, 14 were caught in Florida waters, 6 in Alabama, 60 in Mississippi, 26 in Louisiana, and 7 in Texas; location data could not be obtained for two fish, but they were probably caught in either Mississippi or Louisiana waters. We observed, as had Lotz et al.,[2] that cobia oocyte production appeared to be group synchronous as defined by Wallace and Selman (1981), such that each ovary examined contained oocytes at different stages of maturation. However, ovaries could be assigned to specific categories based on the dominant oocyte maturity stage.

In stage-1 previtellogenesis, the oocytes were small, compact, and irregularly shaped (Fig. 2A). The previtellogenic stage comprised three substages: a) early previtellogenesis, characterized by small oocytes in which the nucleus had swollen to form a large germinal vesicle; b) middle previtellogenesis, characterized by nucleoli developing within the nucleus and causing evaginations to form in the nuclear envelope; and c) late previtellogenesis, characterized by the presence of cortical alveoli. The latter substage marked the beginning of the transition to stage 2.

In stage-2 vitellogenesis, the oocytes increased in size as the yolk material increased (Fig. 2B) and formed unevenly dispersed lipid vacuoles. Vitellogenic oocytes were somewhat more rounded and were not as compacted as previtellogenic oocytes.

During stage-3 final maturation, the oocytes were larger and the lipid vacuoles and proteinaceous yolk material had become more evenly dispersed (Fig. 2C). The lipid droplets fused and congregated around the periphery of the oocytes, resulting in a clearing of that region of the cell. Note that although most of the oocytes in Fig. 2C were stage-3 oocytes; some stage-1 oocytes and late stage-2 oocytes were also present. Chromosomes condensed during stage 3 for the initiation of meiosis (Fig. 2D).

During stage-4 postovulation, unspent oocytes and postovulatory follicles (POF) were resorbed (Fig. 3A). The oocytes became distorted and compacted, as did the POF. Residual lipid vacuoles were observed in the resorbing oocytes. (A few early previtellogenic oocytes can also be seen in Figure 3A, concurrent with the resorption process.)

A sequential round of ovarian development was observed in some cobia ovaries categorized as stage 1' (Fig. 3B). The presence of resorbing oocytes and POF in ovaries suggested that a prior spawning episode had recently occurred. Early previtellogenic oocytes, resorbing oocytes, and POF were not seen simultaneously in ovaries categorized as stage 1. A sequential vitellogenic stage, stage 2', characterized by oocytes with numerous small lipid vacuoles, was also observed (Fig. 3C). Previtellogenic and resorbing oocytes as well as resorbing POF were also present in the ovary during this stage.

Timing of ovarian development

The stages of cobia ovarian development were tabulated according to month of capture for 1991 and 1992 data combined (Table 2). In both April and May, 14–15% of the ovaries were developing (stages 1 and 2), ~60% of the ovaries were ripe and about to be spawned (stage 3), ~20% were postspawning (stage 4), and 3–5% had already spawned but were preparing for a sequential spawning episode (stages 1' and 2'). The similarity in ovarian developmental stages for these two months is not surprising because all the April fish were collected in the last week of the month whereas all the May fish were collected in the first week of that month. During July (first and second weeks of the month), again ~15% of the ovaries were developing (stages 1 and 2) but only ~30% were ripe (stage 3); 15% were postspawning (stage 4) and over 40% had already spawned at least once and were in the process of developing for a subsequent spawning (stages 1' and 2'). Fewer numbers of fish were collected in August (last week of the month) and September (first week of the month) but the predominant stages of ovarian development were dramatically different from fish collected earlier in the season. The majority of ovaries (over 80%) were previtellogenic or vitellogenic (stages 1, 2, and 2') whereas fewer than 20% were ripe (stage 3) or postspawn (stage 4); no stage-1' ovaries were seen.

Gonosomatic index

Cobia with ovaries in stages 1, 2, and 3 had increasing mean GSI's of 1.1 ± 0.6, 5.0 ± 2.2, and 5.4 ± 2.2, respectively (Fig. 4A). GSI declined to 3.5 ± 1.6 in cobia with stage-4 ovaries (postovulation); the lower GSI reflects the loss of oocytes to spawning. Almost all of the pairwise comparisons were significantly different (Tukey-type multiple comparison test,

$\alpha<0.05$). The exceptions were that stage-1 ovaries were not significantly different from stage-1' or stage-2' ovaries nor were stage-1' ovaries significantly different from stage-2' ovaries.

Mean GSI of female cobia was low in both January and March (1.1 ± 0.2 for each month) (Fig. 4B). The January fish were caught on the winter grounds in south Florida waters whereas the March fish were early arrivals in Mississippi waters. GSI increased to 5.5 ± 2.9 in April but declined slightly in May to 4.7 ± 2.0; the largest number of cobia enter Mississippi waters during these two months.[1] Mean GSI continued to decline during July (2.9±1.9) and August (1.7±1.6). Slightly more than half of the pairwise comparisons showed significant differences (Tukey-type multiple comparison test, $\alpha<0.05$). The GSI of January and March fish was significantly different from April, May, and July fish; the GSI of April and May fish was significantly different from July, August, and September fish; and the July and August fish were significantly different from each other.

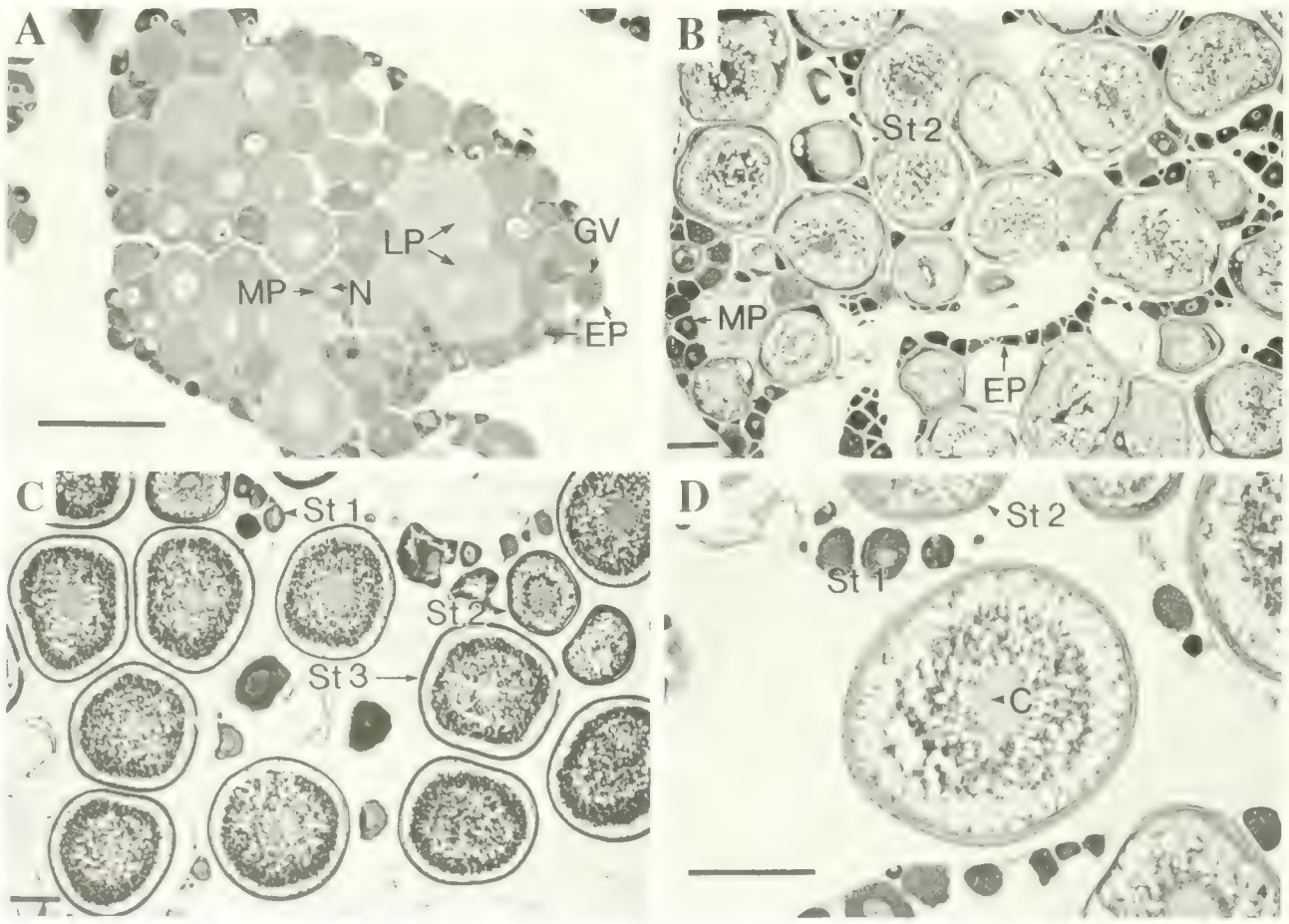

Figure 2

(**A**) Stage-1 cobia, *Rachycentron canadum*, ovary, previtellogenesis. Early previtellogenesis (EP) with large germinal vesicle (GV) developing; middle previtellogenesis (MP) characterized by developing nucleoli (N) which cause evaginations to form in the nuclear envelope; late previtellogenesis (LP) characterized by appearance of lipid vacuoles. (**B**) Stage-2 ovary, vitellogenesis. Vitellogenic oocytes (st 2) have increased in size and in number of lipid vacuoles. Note nonsynchronous formation of oocytes; early previtellogenic (EP) and middle previtellogenic (MP) stage 1 oocytes also occur. (**C**) Stage-3 ovary, final maturation. Oocytes (st 3) enter pre-ovulation stage and become more rounded. Lipid vacuoles concentrate around periphery and cause a clearing. Stage-1 (St 1) and stage-2 (St 2) oocytes are also present. (**D**) Detail of stage-3 ovary. Lipid vacuoles are aggregated around oocyte periphery. Chromosomes (C) condense for initiation of meiosis. Stage-1 (St 1) and late stage-2 (St 2) oocytes are also present. Scale bars=250 µm.

Biochemistry

Biochemical analyses were performed on about one third of the fish sampled for the histological study (n=43). Protein was the major biochemical component (Fig. 5A), representing from 49 to 55% of the ovary total dry weight (507.5–550.5 µg/mg dry weight). There were no statistically significant differences in protein concentration among ovarian developmental stages (Kruskal-Wallis, α>0.05).

Lipid concentration ranged from 209.3 to 412.5 µg/mg dry weight (21–41% dry weight) during ovarian development, increasing from stage 1 through stage 3 (Fig. 5B). The increase was likely due to the formation of lipid yolk during oocyte maturation. Lipid concentrations then decreased after ovulation but not to the low level of stage 1, probably reflecting the residual lipid that had not been resorbed during stage 4. The only statistically significant difference in lipid concentration during the course of ovarian development was between stages 1 and 3 (Tukey-type multiple comparison test, α<0.05).

Carbohydrate concentration was very low during all stages of oogenesis in cobia, ranging from 27.2 to 45.2 µg/mg dry weight (3–4% dry weight) (Fig. 5C). It decreased from stage 1 to 2, increased from stages 3 through 1', and declined slightly in stage 2'. Almost all of the pairwise comparisons of carbohydrate concentration were significant (Tukey-type multiple comparison test, α<0.05) except that stage 1 was not significantly different from stages 4 and 2' nor was stage 2 significantly different from stage 3.

Ash concentration decreased from a high of 196.3 µg/mg dry weight to a low of 55.3 µg/mg dry weight (6–20% dry weight) (Fig. 5D); it increased in stage 4 and stage 1' but declined again in stage 2'. Stage-1 ash concentration was significantly different from stages 3, 4, and 2'; whereas stage 2 was significantly different from stage 3 (Tukey-type multiple comparison test, α<0.05). All of the other pairwise comparisons were not significant.

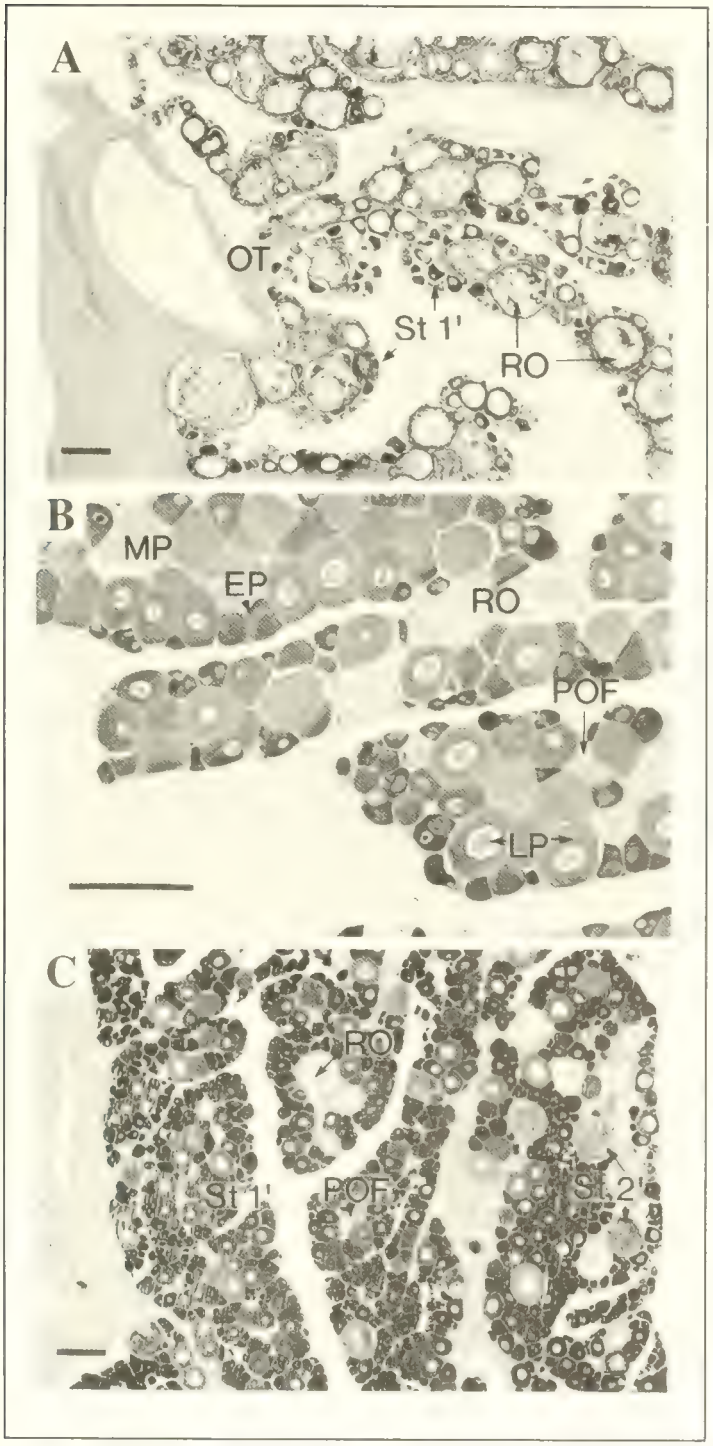

Figure 3

(**A**) Stage-4 ovary, postovulation. Resorption of unspent stage-3 oocytes (RO) into ovarian tissue (OT); oocytes are distorted and compacted. There is residual lipid in the resorbing oocytes. Stage-1' oocytes (St 1') occur. (**B**) Stage-1' ovary, second previtellogenesis. Early previtellogenic (EP), middle previtellogenic (MP), and late previtellogenic (LP) stage-1' oocytes develop. Resorbing oocyte (RO) and resorbing postovulatory follicle (POF) are remnants from stage 4. (**C**) Stage-2' ovary, second vitellogenesis (early). Formation of second round of vitellogenic oocytes (St 2'). Note resorbing oocytes (RO), postovulatory follicles (POF), and stage-1' oocytes (St 1'). Scale bars=250 µm.

Discussion

Protein was the major constituent of cobia ovaries and its contribution remained fairly constant (49–55%) throughout all stages of gonadal devel-

Table 2

Percentage of cobia, *Rachycentron canadum*, ovaries at each stage of development by month of capture. Stages are as described in Table 1. Data are combined from 1991 and 1992.

	Month of capture					
Stage	Apr (n=21)	May (n=58)	Jul (n=27)	Aug (n=6)	Sep (n=6)	Total (n=118)
1	—	5.2	3.7	50.0	66.7	9.3
2	14.3	10.3	11.1	16.7	16.7	11.9
3	61.9	60.3	29.6	—	16.7	48.3
4	19.0	20.7	14.8	16.7	—	17.8
1'	4.8	—	29.6	—	—	7.6
2'	—	3.4	11.1	16.7	—	5.1

opment. We believe that any putative increase in the proteinaceous yolk as oocytes ripened was not detectable by the methods used in this study because the follicles were also increasing in size as oocytes matured. That is, protein concentration was relatively stable because structural protein (follicles, etc.) contributed far more to the total protein concentration than did yolk proteins.

Lipid was the second most abundant component but the levels changed from stage to stage, ranging from 21 to 41%. The fluctuations in lipid concentration during ovarian maturation can be explained by the increasing amount of lipid yolk reserves that are deposited as oocytes mature from stages 1 to 3 followed by the subsequent loss of ripe oocytes from the ovary after ovulation and spawning.

Carbohydrate was the least abundant component (3–4%) of cobia ovaries and ash ranked third (6–20%). Boulekbache (1981) noted that the enzymes of carbohydrate metabolism increased in activity during oogenesis. Carbohydrate concentration, therefore, may be low due to constant catabolism. In the present study, it is not known whether carbohydrate was constantly being catabolized and replaced, or whether concentrations were low. In most fish, however, carbohydrate is not readily available for use until after fertilization occurs (Boulekbache, 1981). The trend in ash concentrations was the inverse of lipid concentrations; that is, ash concentration declined when the lipid concentration increased and vice versa.

Results of biochemical analysis of ripe ovaries from similar studies using other species of fish are given in Table 3. Protein was the major component of ripe ovaries followed by lipid, ash, and carbohydrate for cobia, *Rachycentron canadum* (this study), striped mullet, *Mugil cephalus* (Lu et al., 1979), plaice, *Pleuronectes platessa* (Dawson and Grimm, 1980), and Atlantic cod, *Gadus morhua* (Kjesbu et al., 1991). The primary differences among the four species of fish were the relative proportions of protein and lipid. Ripe cod ovaries had less than half the amount of lipid than either mullet or cobia; cobia ovaries had ~1.1 times more lipid than mullet ovaries. Only for the anabantid *Trichogaster pectoralis* (Hails, 1983) was lipid the major component of ripe ovaries.

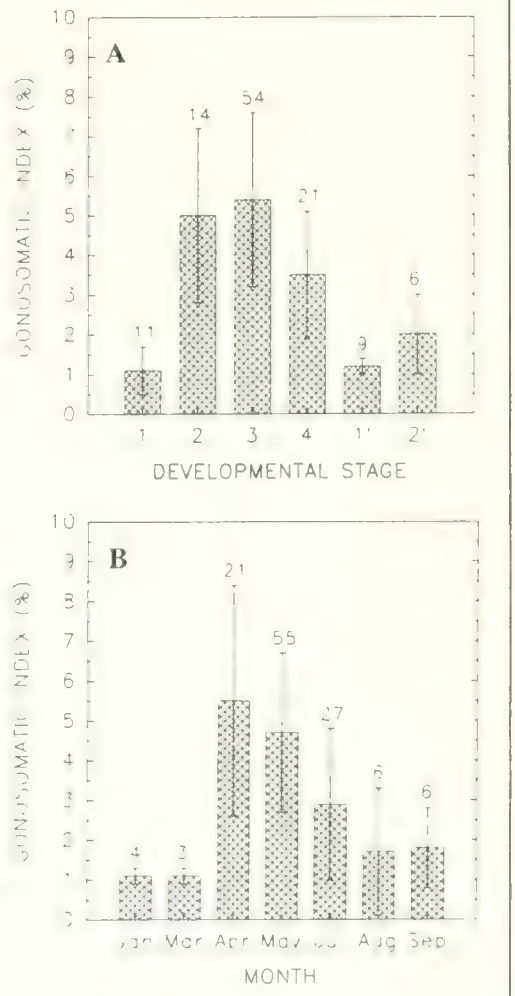

Figure 4

(**A**) Gonosomatic index (mean ± standard deviation) of cobia, *Rachycentron canadum*, in relation to stage of ovarian development. (**B**) Gonosomatic index (mean ± standard deviation) of cobia in relation to month of capture. Numbers above error bars are sample sizes.

Since lipid is the most efficiently stored energy reserve, supplying 9.5 cal/mg, whereas protein liberates 5.7 cal/mg and carbohydrate 4.1 cal/mg (Crisp, 1984), one might expect fish eggs to have large amounts of lipid to supply the energy needed for growth and metabolism during embryogenesis and

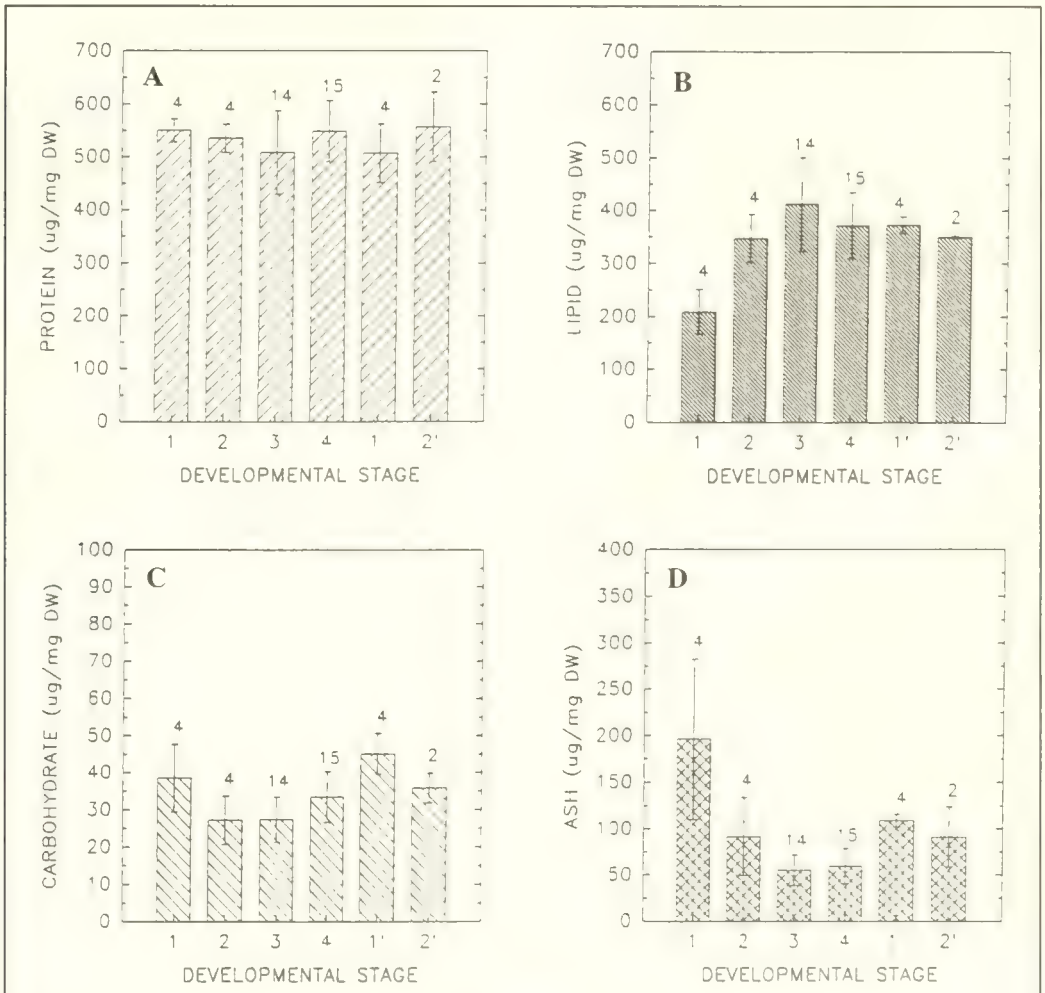

Figure 5

(**A**) Mean protein concentration (µg protein/mg dry weight (DW) ± standard deviation) in developing cobia, *Rachycentron canadum,* ovaries. (**B**) Mean lipid concentration (µg lipid/mg dry weight ± standard deviation). (**C**) Mean carbohydrate concentration (µg carbohydrate/mg dry weight ± standard deviation); note change in Y-axis scale. (**D**) Mean ash concentration (µg ash/mg dry weight ± standard deviation); note change in Y-axis scale. 1=stage-1 previtellogenesis; 2=stage-2 vitellogenesis; 3=stage-3 final maturation; 4=stage-4 postovulation; 1'=stage-1' sequential previtellogenesis; 2'=stage-2' sequential vitellogenesis. Numbers above error bars are sample sizes.

subsequent early larval development before first-feeding. The lipid:protein (L:P) ratio of ripe cobia oocytes (not ovaries as reported in the present study) was 1: 0.7 (Caylor, 1992), which is similar to both striped bass, *Morone saxatilis,* eggs (1: 0.6) (Eldridge et al., 1982) and red drum, *Sciaenops ocellatus,* eggs (1:0.8) (Vetter et al., 1983). Winter flounder, *Pseudopleuronectes americanus,* eggs, however, had a much higher L:P ratio of 1:5.2 (Cetta and Capuzzo, 1982).

One factor affecting the storage of biochemical components is egg size. Many marine fish eggs are relatively small and do not have large stores of energetic reserves; these small eggs usually hatch quickly. Cobia eggs range from 1.16 to 1.42 mm in diameter (Joseph et al., 1964). Red drum eggs are 0.86–0.98 mm (Vetter et al., 1983) and striped bass oocytes are 3.3–3.4 mm after hydration (Eldridge et al., 1981). Winter flounder eggs are the smallest, 0.74–0.85 mm diameter (Smigielski and Arnold, 1972), yet they are composed of about five times as much protein as lipid. Thus, generalizations about energy reserve storage cannot be made based solely on egg size.

Winter flounder eggs are demersal whereas eggs of cobia, red drum, and striped bass are pelagic. De-

Table 3

Biochemical composition (% dry weight) of some fish ovaries including cobia, *Rachycentron canadum*.

Species	Protein	Lipid	Carbohydrate	Ash	Reference
Rachycentron canadum (cobia)					
(ripe ovary)	50.7	41.1	2.7	5.5	present study
Mugil cephalus (mullet)					
(ripe ovary)	59.3	36.0	—	4.7	Lu et al., 1979[1]
Pleuronectes platessa (plaice)					
(ripe ovary)	87.4	8.4	—	3.1	Dawson and Grimm, 1980[2]
(spent ovary)	88.6	3.6	—	7.1	Dawson and Grimm, 1980[2]
Trichogaster pectoralis (anabantid)					
(ripe ovary)	27.7	72.3	0.16	—	Hails, 1983[2]
Gadus morhua (Atlantic cod)					
(ripe ovary)	77.7	16.5	0.7	5.1	Kjesbu et al., 1991[1]

[1] Original data reported as percent wet weight; we converted to percent dry weight.
[2] Original data reported as dry weight; we converted to percent dry weight

mersal eggs tend to have more protein than lipid (Flachter and Pandian, 1968), which results in negative buoyancy. This could account for the high proportion of protein in winter flounder eggs in contrast to the high proportion of lipid in cobia, striped bass, and red drum eggs. Another possible explanation for the two very different patterns of biochemical composition is that cobia, striped bass, and red drum are warm-temperate species whereas winter flounder is a cold-water species. Cobia (Ditty and Shaw, 1992), striped bass (Harrell et al., 1990), and red drum (Vetter et al., 1983) have short incubation times: 24 hours at 29°C, 48 hours at 18°C, and 22 hours at 23°C, respectively. Winter flounder has a much longer incubation time, 11–20 days at 4–6°C (Cetta and Capuzzo, 1982). The difference in incubation times for different species is due in part to the effect of temperature on metabolic rate of the developing embryos. Catabolism of specific endogenous energy stores in fish eggs is known to be related to the temperature of incubation. Lipid tends to be consumed in higher quantities at higher temperatures but protein consumption dominates at lower temperatures (Heming and Buddington, 1988). Therefore, it is not surprising to see different patterns of biochemical composition in light of the temperature history during early development of these different species.

In addition to reporting the changes in biochemical composition during cobia ovarian development, we also examined the cyclical variation in ovary size. This was done by means of the gonosomatic index (GSI), a commonly used ratio that normalizes gonad size among animals of different size classes in order to assess their reproductive state. The GSI was determined for each female cobia sampled in this study and compared both to stage of ovarian development and to month of capture. The majority of cobia landed in April and May had ovaries in stage-3 condition (~60%). This was reflected in the high mean GSI for those months. By July and August fewer cobia, ~30% and 0%, respectively, had stage-3 ovaries; this was reflected by the declining mean GSI. In September the increase in cobia with ovaries in prespawning condition was indicated by the slight increase in GSI.

It is not clear why there was a greater proportion of stage-1 and stage-2 ovaries in August and September. Possible explanations include 1) difficulty in distinguishing stage-2 ovaries from stage-2' ovaries; 2) presence of resident young, small fish that were immature at the beginning of the summer but which grew to maturity late in the season; or 3) an influx of older, late-arriving cobia from unknown areas. We believe that a combination of the first two explanations is most likely. Some of the late summer/early fall fish with ovaries classified as stage-2 fish may well have spawned a batch of eggs earlier in the season and therefore were actually stage 2'. But after the POF and any unspent stage-3 oocytes are resorbed, it is not possible to distinguish between a stage-2 and stage-2' ovary. On the other hand, the late summer and early fall stage-1 fish were small; fork length was 94.8 ± 5.3 cm and 102.8 ± 7.9 cm in August and September, respectively. Based on cobia growth equations,[2] it is highly unlikely that these fish could have spawned the previous year, and they were probably too immature to have spawned earlier in the same year. It is not known whether these fish would have spawned in the fall or whether they would have overwintered without further ovarian development.

Lotz et al.[2] suggested that cobia spawn over some unspecified period of time during the May to Sep-

tember season. Their conclusion was based on the observed nonsynchronous formation of oocytes in the ovaries, considered to be strong evidence of multiple spawning (Hunter et al., 1992). Nonsynchronous development of oocytes was also observed in the present study. Data from this study further suggest that cobia resorb unspent stage-3 oocytes after ovulation. This hypothesis is supported both by the biochemical data and the histological evidence of residual lipid in stage-4 and stage-1' ovaries.

In summary, we have determined that lipid concentration, but not protein concentration, changes during cobia ovarian development, presumably as lipid yolk reserves are deposited in the oocytes. Carbohydrate and ash concentrations also varied during development, but they were only minor components of the system. Further research is needed on newly fertilized cobia eggs and developing embryos and larvae in order to answer questions about the patterns and rates of energy reserve utilization during embryogenesis and during larval development before first feeding in this species. Because cobia eggs and larvae are only rarely found in plankton collections in the Gulf of Mexico, we have initiated studies on the spawning of ripe, field-caught cobia (Caylor et al., in press).

Acknowledgments

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Literature cited

Blaxter, J. H. S.
1969. Development: eggs and larvae. *In* W. S. Hoar and D. J. Randall (eds.), Fish physiology, Vol. III, p. 179–252. Academic Press, New York.

Bligh, E. G., and W. J. Dyer.
1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37:911–917.

Boulekbache, H.
1981. Energy metabolism in fish development. Am. Zool. 21:377–389.

Briggs, J. C.
1958. A list of Florida fishes and their distribution. Bull. Fla. State Mus. Biol. Sci. 2:1–318.

Caylor, R. E.
1992. Histological and biochemical aspects of the developing ovary of *Rachycentron canadum* (Linnaeus). M.S. thesis, Univ. Southern Mississippi, Hattiesburg, MS, 85 p.

Caylor, R. E., P. M. Biesiot, and J. S. Franks.
In press. Culture of cobia *Rachycentron canadum*: cryopreservation of sperm and induced spawning. Aquaculture.

Cetta, C. M., and J. M. Capuzzo.
1982. Physiological and biochemical aspects of embryonic and larval development of the winter flounder *Pseudopleuronectes americanus*. Mar. Biol. 71:327–337.

Crisp, D. J.
1984. Energy flow measurements. *In* N. A. Holme and A. D. McIntyre (eds.), Methods for the study of marine benthos, p. 284–372. Blackwell Scientific Publs., Oxford.

Dawson, A. S., and A. S. Grimm.
1980. Quantitative seasonal changes in the protein, lipid and energy content of the carcass, ovaries and liver of adult female plaice, *Pleuronectes platessa* L. J. Fish. Biol. 16:493–504.

Dawson, C. E.
1971. Occurrence and description of prejuvenile and early juvenile Gulf of Mexico cobia, *Rachycentron canadum*. Copeia 1971:65–71.

DeVlaming, V., G. Grossman, and F. Chapman.
1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. 73A:31–39.

Ditty, J. G., and R. F. Shaw.
1992. Larval development, distribution, and ecology of cobia *Rachycentron canadum* (Family: Rachycentridae) in the northern Gulf of Mexico. Fish. Bull. 90:668–677.

Dubois, M., K. A. Gilles, J. K. Hamilton, P. A. Rebers, and F. Smith.
1956. Calorimetric method for determination of sugars and related substances. Anal. Chem. 28: 350–356.

Eldridge, M. B., J. Whipple, and D. Eng.
1981. Endogenous energy sources as factors affecting mortality and development in striped bass (*Morone saxatilis*) eggs and larvae. Rapp. P-V. Reun. Cons. Int. Explor. Mer 178:568–570.

Eldridge, M. B., J. A. Whipple, and M. J. Bowers.
1982. Bioenergetics and growth of striped bass, *Morone saxatilis*, embryos and larvae. Fish. Bull. 80:461–473.

Flachter, J., and T. S. Pandian.
1968. Rate and efficiency of yolk utilization in developing eggs of the sole (*Solea solea*). Helgol. Wiss. Meeresunters. 18:53–60.

Folch, J., M. Lees, and G. H. Sloane Stanley.
1957. A simple method for the isolation and purification of total lipides (*sic*) from animal tissues. J. Biol. Chem. 226:497–509.

Guraya, S. S.
1986. The cell and molecular biology of fish oogenesis. Karger Press, New York, 223 p.

Hails, A. J.
1983. Temporal changes in fat and protein levels in the tropical anabantid *Trichogaster pectoralis* (Regan). J. Fish. Biol. 22:203–213.

Harrell, R. M., J. H. Kerby, and R. V. Minton, eds.
1990. Culture and propagation of striped bass and its hybrids. Striped Bass Committee, Southern Div., Am. Fish. Soc., Bethesda, MD.

Hartree, E. F.
1972. Determination of protein: a modification of the Lowry method that gives a linear photometric response. Anal. Biochem. 48:422–427.

Heming, T. A., and R. K. Buddington.
1988. Yolk absorption in embryonic and larval fishes. *In* W. S. Hoar and D. J. Randall (eds.), Fish physiology, Vol. XI, p. 407–446. Academic Press, Inc., New York.

Humason, G. L.
1979. Animal tissue techniques. W.H. Freeman and Co., San Francisco, 661 p.

Hunter, J. R., B. J. Macewicz, N. C. Lo, and C. A. Kimbrell.
1992. Fecundity, spawning, and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull. 90:101–128.

Joseph, E. B., J. J. Norcross, and W. H. Massmann.
1964. Spawning of the cobia, *Rachycentron canadum*, in the Chesapeake Bay area, with observations of juvenile specimens. Chesapeake Sci. 5:67–71.

Kjesbu, O. S., J. Klungsoyr, H. Kryvi, P. R. Witthames, and M. Greer Walker.
1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. 48:2333–2343.

Lu, J. Y., Y. M. Ma, C. Williams, and R. A. Chung.
1979. Fatty and amino acid composition of salted mullet roe. J. Food Sci. 44:676–677.

Migdalski, E. C., and G. S. Fichter.
1983. Family Rachycentridae: cobia. *In* The fresh and salt water fishes of the world, p. 225–226. Crown Publishers, Inc., New York.

Mommsen, T. P., and P. J. Walsh.
1988. Vitellogenesis and oocyte assembly. *In* W. S. Hoar and D. J. Randall (eds.), Fish physiology, Vol. XI, p. 347–406. Academic Press, Inc., New York.

Overstreet, R.
1983a. Aspects of the biology of the red drum, *Sciaenops ocellatus*, in Mississippi. Gulf Res. Rep. Supplement 1:45–68.
1983b. Aspects of the biology of the spotted seatrout, *Cynoscion nebulosus*, in Mississippi. Gulf Res. Rep. Supplement 1:1–43.

Richards, C. E.
1967. Age, growth and fecundity of the cobia, *Rachycentron canadum*, from Chesapeake Bay and adjacent mid-Atlantic waters. Trans. Am. Fish. Soc. 96:343–350.
1977. Cobia (*Rachycentron canadum*) tagging within Chesapeake Bay and updating of growth equations. Chesapeake Sci. 18:310–311.

Sasaki, G. C., and J. M. Capuzzo.
1984. Degradation of *Artemia* lipids under storage. Comp. Biochem. Physiol. 78B:525–531.

Smigielski, A. S., and C. R. Arnold.
1972. Separating and incubating winter flounder eggs. Prog. Fish-Cult. 34:113.

Vetter, R. D., R. E. Hodson, and C. Arnold.
1983. Energy metabolism in a rapidly developing marine fish egg, the red drum (*Sciaenops ocellata*). Can. J. Fish. Aquat. Sci. 40:627–634.

Wallace, R. A., and K. Selman.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

Zar, J. H.
1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ, p. 138–145.

Seasonal cycles in the sonic muscles of the weakfish, *Cynoscion regalis*

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Abstract.—Male weakfish, *Cynoscion regalis*, were collected from the southwest portion of Delaware Bay from April through September in 1990 and 1991. Morphometric measurements of the sonic muscles, testis size (gonadosomatic index, or GSI), and plasma androgen concentrations were recorded to obtain data on the seasonality of sonic muscle condition and its relationship with the timing of reproduction in this population. The sonic muscles were bilaterally symmetrical and showed no significant seasonal differences in length or width across both collecting periods. Sonic muscle thickness did change significantly across both collecting periods and there was a threefold increase in sonic muscle mass during the course of each collecting period. GSI and levels of both plasma testosterone and 11-ketotestosterone also varied significantly across both collecting seasons. Changes in sonic muscle mass followed but lagged one to three weeks behind the rise and fall in plasma androgen levels. Pertinent models of skeletal muscle hypertrophy and atrophy are discussed as is the possibility that increased sonic muscle mass during the spawning season may increase the reproductive fitness of male weakfish.

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Sound production is used by a number of teleost species during aggressive or defensive behaviors (Gray and Winn, 1961; Steinberg et al., 1965; Hawkins and Chapman, 1966; Horch and Salmon, 1973; Hawkins and Rasmussen, 1978), but the greatest volumes of sound produced by teleosts are associated with reproduction. A number of marine families including Batrachoididae (Gray and Winn, 1961; Fish, 1964), Blenniidae (Tavolga, 1958b), Gadidae (Hawkins and Rasmussen, 1978), Gobiidae (Tavolga, 1958a), Triglidae (Moulton, 1956), Sciaenidae (Hildebrand and Schroeder, 1928; Pearson, 1929; Burkenroad, 1931), Serranidae, and Scaridae (Lobel, 1992) produce sound during the spawning season. Choruses of these sounds are generally limited to the season and geographic area in which the species in question spawns (Fish and Cummings, 1972; Fine, 1978; Takemura et al., 1978; Mok and Gilmore, 1983; Saucier and Baltz, 1993).

Teleostean sound production is generally accomplished through one of three mechanisms: hydrodynamic sound production via movement through the water, stridulation of bony body parts, or the use of specialized drumming muscles. The latter two mechanisms are often amplified by sympathetic vibration of the swim bladder, especially in the case of the drumming or sonic muscles. The sonic muscles may be intrinsic or extrinsic to the swim bladder. Intrinsic sonic muscles originate and insert entirely on the swim bladder, and appear as a part of the swim bladder wall. Extrinsic sonic muscles, however, originate on the cranium, pectoral girdle, or lateral body wall musculature and insert on or near the swim bladder (Tavolga, 1964; Demski et al., 1973).

Male sciaenids produce a 'drumming' sound through the use of sexually dimorphic, extrinsic sonic muscles. The Atlantic croaker, *Micropogonias undulatus*, is the only member of this family in which the sonic muscles are found in both the male and female (Smith, 1905; Tower, 1908; Fish and Mowbray, 1970; Hill et al., 1987). The drumming behaviors of sciaenid species are primarily limited to the reproductive periods of these species (Fish and Cummings, 1972; Takemura et al., 1978; Mok and Gilmore, 1983; Saucier and Baltz, 1993). Male drumming in sciaenids is believed to play a role in the spawning behavior of these species (Pearson, 1929; Guest and Lasswell, 1978; Thomas[1]).

[1] D. L. Thomas. 1971. The early life history and ecology of six species of drum (Sciaenidae) in the lower Delaware River, a brackish tidal estuary. Ichthyological Associates, Delaware Progress Rep. 3 (Part III), 247 p.

The weakfish, *Cynoscion regalis*, is a sciaenid which spawns in bays and estuaries from North Carolina to Long Island, New York, during the spring and early summer (Welsh and Breder, 1923; Mercer, 1983). Merriner (1976) noted a change in the coloration of the sonic muscles in male weakfish that paralleled the changes in testis condition during the course of the year.

The purpose of the present study was to determine whether the condition of the sonic muscles of male weakfish changes seasonally. In particular, this study was designed to determine the extent of change, if any, in the morphometrics of the sonic muscles over the course of the spawning season and to observe these variations in relation to changes in testis condition and plasma androgen levels.

Materials and methods

Sample collection

Male weakfish were sampled near the mouth of the Delaware Bay (lat. 38°50.30'N, long. 075°12.92'W) and roughly 40 km north of this (39°11.98'N, 075°23.20'W). Field collections were made from May through September in 1990 and from April through September in 1991. Specimens were collected by means of anchored or drifting gill nets, hook and line, and otter trawl.

Immediately after capture of the fish, blood samples were taken with heparinized syringes from the hemal canal, posterior to the anal fin. The blood was then placed in heparinized microcentrifuge tubes and stored on ice. Samples were centrifuged at 2,000 × g, and the supernatant was removed and frozen at –80°C for determination of plasma testosterone and 11-ketotestosterone levels via radioimmunoassay (RIA). In 1991, blood sampling was preceded by milt collection to determine the number of ripe specimens. Any drumming behavior was also noted.

Autopsies of the specimens provided total length (TL), total weight (TW), testis weight, and morphometric measurements of the sonic muscles. Testis weight and total weight were used to calculate a gonadosomatic index (GSI={total testis weight/total weight} × 100). Sonic muscle weight, width (anterior-posterior axis of the muscle), length (dorso-ventral axis of the muscle), and maximal thickness (cross-section of the muscle) were measured for both the right and left sonic muscles. Orientation of sonic muscle width and length measurements is based on the dorso-ventral orientation of the muscle fibers (Ono and Poss, 1982). The sonic muscle-somatic index (SMSI) was calculated as SMSI = {total sonic muscle weight/total weight × 100}, and the results were expressed as a percentage of TW. Indices for sonic muscle width (SMWI), length (SMLI) and thickness (SMTI) were calculated as the mean of the measurement for the right and left sonic muscles/total length × 100 and were expressed as a percentage of TL. The color of the sonic muscles was also noted.

Radioimmunoassays

Testosterone was measured by direct radioimmunoassay. Five µL aliquots of serum were placed in 2-mL conical glass tubes (methanol rinsed) and diluted to a total volume of 50 µL with borate buffer. Diluted samples were incubated at 60°C for one hour to dissociate the steroid from binding proteins. Standard solutions were prepared by dissolving crystalline testosterone (Sigma Chemical Co., St. Louis, MO) in absolute ethanol. Working standards (5, 10, 25, 50, 100, 250, 500 pg testosterone 5 μL^{-1}) were prepared in ethanol, dried to zero volume at 45°C under vacuum, and reconstituted in 50 µL of borate buffer. Standards and sample tubes were incubated with 100 µL (approximately 4,000 cpm) of dilute trace (1,2,6,7-^{3}H testosterone, cat. #NET-370, New England Nuclear Corporation) and 100 µL of reconstituted antiserum (Wein Laboratories, Succasunna, NJ) overnight at room temperature. Total counts were estimated by using vials containing 100 µL of dilute trace and 100 µL of saturated ammonium sulfate. Triplicate standard and serum samples incubated without the addition of antiserum were used to calculate nonspecific binding. Bound steroids were precipitated by adding 250 µL of saturated ammonium sulfate to each tube. The vials were centrifuged and 400 µL of the supernatant were removed and placed in counting vials along with 6 mL of scintillation cocktail. All tubes were shaken for 25 minutes, allowed to sit for at least one hour, and counted for 3–10 minutes in a liquid scintillation counter.

Testosterone measurements were assumed to estimate total testosterone levels, as the plasma was incubated at 60°C for one hour to dissociate any binding proteins in the plasma. The 11-ketotestosterone assay (Woods and Sullivan, 1993) measured only free, or unbound, steroid, as the protocol includes triplicate ethyl-ether extraction of unbound steroids from the plasma.

Cross-reactivities of the testosterone antiserum were ≥50% for 5α-dihydrotestosterone and δ-1-testosterone, approximately 18% and 12.5% for 5α-androsten-3β,17β-diol and δ-5-androsten-3β,17β-diol, respectively, and <5% for all other steroids tested (Wein Laboratories, Inc.). Tritiated 11-ketotestosterone and 11-ketotestosterone antiserum were gifts

from C. V. Sullivan (Dept. Zoology, North Carolina State University, Raleigh, North Carolina). This antiserum cross-reacted less than 2% with testosterone (Hourigan et al., 1991).

Extraction efficiencies for the 11-ketotestosterone assay, determined by extraction of samples spiked with a known amount of radiolabelled 11-ketotestosterone, were always greater than 85%. RIA parallelism was determined by measurement of various equivalents of plasma from a single plasma pool. The results were parallel to the standard curve over a range of 1–20 µL plasma for the testosterone assay and 25–250 µL plasma for the 11-ketotestosterone assay (sample sizes for the assays were 5 and 50 µL, respectively). When a range of steroid concentrations was added to plasma pool samples of known hormone concentration, the quantities of spiked steroid recovered were not significantly different from the quantities added for either assay. The intra- and inter-assay coefficients of variation were, respectively, 10.3% and 18.5% for the testosterone assay and 7.4% and 17.1% for the 11-ketotestosterone assay.

Statistical analyses

Specimens with a TL outside a 15-cm range around the sample mean for each year were not included in this analysis. This limited size range was used for two reasons: first, to alleviate the possible effects of allometric growth on the indices used to present the data; and second, to remain within the size range of two- and three-year-old weakfish used by Villoso (1989). The calculated indices, such as GSI, were used only to display the data. Statistical analyses on testis weight and sonic muscle morphometric measurements were conducted by using analyses of covariance with TW or TL of the specimen considered as a covariate. Bilateral comparisons of sonic muscle morphometrics were made by using a paired *t*-test. Statistical analyses of plasma androgen levels were accomplished by using a one-way analysis of variance. The α level for these analyses was 0.05.

Results

A difference was noted between 1990 and 1991 surface water temperatures, which rose more rapidly in 1991 (Fig. 1). Surface temperatures reached 26°C by late May in 1991 but not until late June in 1990. The apparent result of these temperature differences was a two-week difference in the course of events across the collecting period so that 1991 trends began earlier than those in 1990.

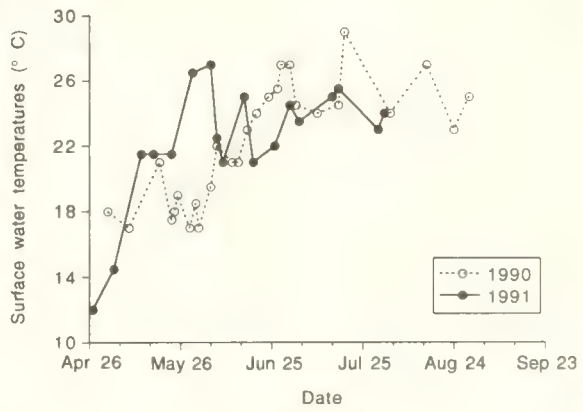

Figure 1

Surface water temperatures in the lower Delaware Bay for the 1990 and 1991 collecting seasons.

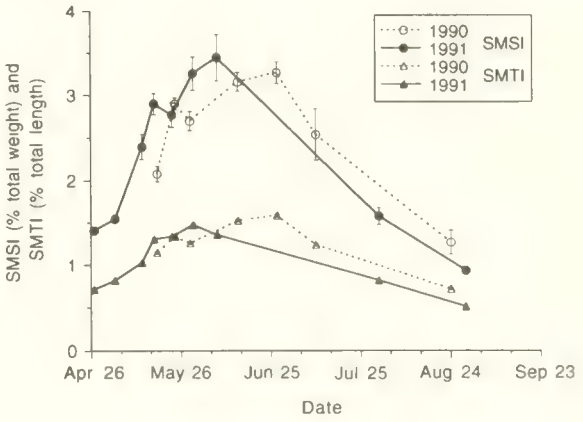

Figure 2

Sonic muscle thickness index (SMTI) and sonic muscle-somatic index (SMSI) of the weakfish, *Cynoscion regalis*, plotted across sampling date for the 1990 and 1991 collecting seasons. Points are means (n=3–10 fish) ± one standard error of the mean.

Sonic muscles were bilaterally symmetrical; we were unable to detect significant differences between the two sides in length, thickness, weight, or color in 1990 or 1991. Sonic muscle width on the left side was significantly longer than that on the right side in 1990, but this trend was not repeated in 1991.

Mean sonic muscle thickness changed significantly across the collecting season in both years. During both collecting periods, SMTI climbed to a peak of approximately 1.5% of TL by late June before steadily decreasing to post-spawning values of approximately 0.6% of TL (Fig. 2). Concurrently, there was a significant seasonal change in total sonic muscle weight in both 1990 and 1991. SMSI values rose to between

3.3 and 3.5% of TW by the peak of the spawning season in both years and decreased to roughly 1% of TW by the fall (Fig. 2). These seasonal changes in SMSI represent a threefold increase in sonic muscle mass.

Sonic muscle color also changed seasonally, following the changes in sonic muscle thickness. The sonic muscles were a dark blood-red throughout May and most of June. During late June and July muscle color faded to a dark pink, and in August to a light pink. During September and October sonic muscle color faded to a dark yellow and the muscle tissue became semitranslucent.

There were no significant seasonal changes in the mean sonic muscle length in either 1990 or 1991. SMLI values remained between 6 and 7% of TL across the entire collecting period during both years. A significant seasonal change in mean sonic muscle width was noted in 1990 but not in 1991. SMWI ranged from 28.6 to 30.8% of TL in 1990 and from only 28.3 to 29.2% of TL in 1991.

Total testis weight changed significantly across the collecting period in both 1990 and 1991. GSI values rose to a maximum of 4.2% of TW in both collecting seasons. After the peak of the spawning season, GSI values decreased rapidly, reaching postspawning lows between 0.1 and 0.2% of TW in the early fall (Fig. 3A).

Plasma androgen levels also varied significantly during both collecting seasons. Total plasma testosterone titers were somewhat lower in 1990, reaching a maximum of only 3.34 ng·mL^{-1}, whereas 1991 values climbed to 5.5 ng·mL^{-1} (Fig. 3B). In both years levels decreased to postspawning values of between 1.2 and 1.6 ng·mL^{-1}. Unbound plasma 11-ketotestosterone levels followed a trend similar to that noted for total plasma testosterone during both collecting periods (Fig. 3C). Maximal levels of unbound 11-ketotestosterone reached 1.1 ng·mL^{-1} in both years and then decreased to less than 0.1 ng·mL^{-1} by the fall.

Examination of weakfish in 1991 indicated that virtually all the specimens were capable of drumming when handled throughout the entire collecting period, regardless of changes in sonic muscle condition. Specimens produced milt throughout most of the study period, although no milt could be obtained before mid-May and none was obtained after mid-August.

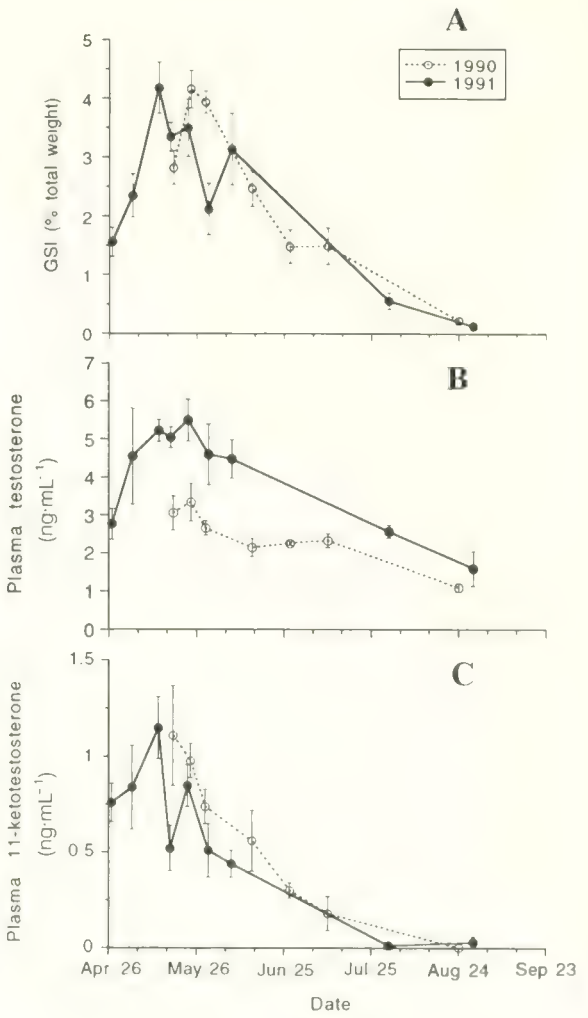

Figure 3

(**A**) Gonadosomatic index (GSI); (**B**) plasma testosterone concentration; (**C**) and unbound plasma 11-ketotestosterone concentration of the weakfish, *Cynoscion regalis*, plotted across sampling date for the 1990 and 1991 collecting seasons. Points are means (n=3–10 fish) ± one standard error of the mean.

Discussion

The extreme seasonality of drumming activity in sciaenids (Fish and Cummings, 1972; Takemura et al., 1978; Mok and Gilmore, 1983; Saucier and Baltz, 1993) suggests that the condition of the sonic muscles in these species may not remain constant throughout the year. The data presented here indicate that the condition of the sonic muscles of weakfish does change seasonally; there was an approximate threefold difference in mass between the spawning and pre- or post-spawning periods. As the sonic muscle could not grow beyond its points of attachment (Tower, 1908; Ono and Poss, 1982), which define the length and width of the muscle, seasonal hypertrophy was expressed as an increase in muscle thickness. Seasonal changes in sonic muscle condition have not been documented in other sciaenids; how-

ever, a seasonal increase was noted in the sonic muscle mass of the male haddock, *Melanogrammus aeglefinus* (Templeman and Hodder, 1958). The sonic muscles of haddock are present in both sexes, but the seasonal increase in volume of the muscles was noted only in the males.

Maximal levels of total plasma testosterone observed in this study ranged between 3.5 and 5.5 $ng \cdot mL^{-1}$. Peak testosterone levels of 2.4 $ng \cdot mL^{-1}$ were noted in the closely related spotted seatrout, *Cynoscion nebulosus*.[2] Similarly, maximal levels of 11-ketotestosterone in the spotted seatrout fell between 8 $ng \cdot mL^{-1}$ and 10 $ng \cdot mL^{-1}$. Unbound 11-ketotestosterone levels in the weakfish, presumably expressing only a fraction of the entire plasma pool of this steroid, were roughly one order of magnitude less than maximal levels in spotted seatrout.

The similarity of the shapes of the androgen and SMSI curves suggests that plasma androgen levels may play a role in the seasonal cycling of the sonic muscle. Seasonal hypertrophy of the sonic muscles appears to be triggered by increasing plasma androgen levels in the spring. Similarly, the increased sonic muscle mass noted during the summer appears to be maintained by high plasma androgen titers. As androgen levels peaked and began to fall, sonic muscle mass continued to increase for a period of one to three weeks, then began to drop off as atrophy directly followed peak mass. There was no plateau in plasma androgen levels, nor was one noted in the plot of changing SMSI. Fine and Pennypacker (1986) noted an increase in the mass and a darkening in the coloration of the sonic muscles of male and female toadfish after gonadectomy and administration of either testosterone or 11-ketotestosterone. Injection of testosterone in male anurans can initiate calling behaviors and has been shown to accentuate the sexual dimorphism of the calling apparatus (Obert, 1977; Sassoon and Kelley, 1986).

In mammals, increased androgen levels can induce increased muscle protein synthesis and muscle glycogen storage, resulting in muscle hypertrophy (Lamb, 1975). Increasing the workload of a muscle can also result in hypertrophy of the muscle. Work-induced hypertrophy can occur in the absence of pituitary growth hormones, insulin, or androgens. Increased muscle mass in work-induced hypertrophy is the result of increased protein concentrations in the tissue. Much of this new protein is myofibrillar and is believed to result in increased cross-sectional area of the muscle fiber (Goldberg et al., 1975). Increases in muscle aerobic enzyme activities, mitochondrial protein concentrations, myoglobin concentrations, and muscle glycogen storage have been noted in exercise-induced hypertrophy in mammals (Holloszy, 1967; Edgerton et al., 1969; Barnard et al., 1970). It is possible that the hypertrophy experienced by the sonic muscles of weakfish in the spring may involve both of these pathways. Data presented here indicate that elevated plasma androgen levels may have played a role in the seasonal increase in mass noted in these muscles. Increasing androgen levels may play a direct anabolic role in muscle hypertrophy, or they may cue work-induced hypertrophy by initiating drumming behaviors, or both. Field hydrophone data from this population collected in 1992 (Connaughton and Taylor, in press) indicate that drumming activity begins approximately 4–6 weeks before maximal sonic muscle mass is reached.

The decreasing mass of the sonic muscles of weakfish in mid- to late-summer may be the result of decreasing androgen levels and decreased workload. Field recordings of voluntary drumming indicated that this behavior ceased abruptly after the spawning season (Connaughton and Taylor, in press). Atrophy caused by disuse in mammalian systems results in a decrease in fiber cross-sectional area and muscle mass (Desplanches et al., 1987; Musacchia et al., 1988). The decreased use of the sonic muscles after the spawning season might result in atrophy and subsequent weight loss in the sonic muscles.

Observations of specimens collected in 1991 suggested that while the sonic muscle condition declined throughout the summer and fall, the specimens were still capable of producing sound when handled. If the sonic muscles were capable of producing sound regardless of their condition, then the seasonal hypertrophy of these muscles must play a role other than activation of the muscles. Muscle hypertrophy in mammals can result in more powerful muscle contractions by that muscle (Goldberg et al., 1975). An increase in the strength of the sonic muscle contraction might increase the amplitude of the drumming call, allowing the male to be heard at greater distances or at increased intensities at a given distance, or both. Also, potential increases in aerobic capacity and in concentration of mitochondria may increase the stamina of the sonic muscles, permitting calling bouts of longer duration.

If male drumming plays a role in weakfish reproductive behavior, the condition of the sonic muscles may affect an individual's reproductive success. However, maintenance of peak condition of this other-

[2] P. Thomas, N. J. Brown, and C. R. Arnold. 1982. Seasonal variations of plasma androgens and gonad histology in male spotted seatrout, *Cynoscion regalis* (Family: Sciaenidae). *In* C. J. J Richter and H. J. T. Goos (eds.), Proceedings of the international symposium on reproductive physiology of fish, p. 111. Centre for Agricultural Publication and Documentation, Wageningen, Netherlands.

wise unused muscle throughout the remainder of the year might consume energy that could otherwise be budgeted toward growth, foraging, or predator avoidance and thus increase the individual's chances of reproducing again. Seasonal hypertrophy and atrophy of the sonic muscles ensure peak mass only at the appropriate time. This cycle is presumably driven by an indicator of the proximity of the spawning season, such as day length and correlated temperature changes, operating through changes in plasma androgen levels.

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Literature cited

Barnard, R. J., V. R. Edgerton, and J. B. Peter.
1970. Effect of exercise on skeletal muscle. I: Biochemical and histological properties. J. Appl. Physiol. 28:762–766.

Burkenroad, M. D.
1931. Notes on the sound-producing marine fishes of Louisiana. Copeia 1931:20–28.

Connaughton, M. A., and M. H. Taylor.
In press. Seasonal and daily cycles in sound production associated with spawning in the weakfish, *Cynoscion regalis*. Env. Biol. Fish.

Demski, L. S., J. W. Gerald, and A. N. Popper.
1973. Central and peripheral mechanisms of teleost sound production. Am. Zool. 13:1141–1167.

Desplanches, D., M. H. Mayet, B. Sempore, and R. Flandrois.
1987. Structural and functional responses to prolonged hindlimb suspension in rat muscle. J. Appl. Physiol. 63:558–563.

Edgerton, V. R., L. Gerchman, and R. Carrow.
1969. Histochemical changes in rat skeletal muscle after exercise. Exp. Neurol. 24:110–123.

Fine, M. L.
1978. Seasonal and geographical variation of the mating call of the oyster toadfish *Opsanus tau*. Oecologia 36:45–57.

Fine, M. L., and K. R. Pennypacker.
1986. Hormonal basis for sexual dimorphism of the sound producing apparatus of the oyster toadfish. Exp. Neurol. 92:289–298.

Fish, M. P.
1964. Biological sources of sustained ambient sea noise. *In* W. N. Tavolga (ed.), Marine bio-acoustics, Vol. 1, p. 175–194. Pergamon Press, New York.

Fish, M. P., and W. H. Mowbray.
1970. Sounds of western North Atlantic fishes. The Johns Hopkins Press, Baltimore, 207 p.

Fish, J. F., and W. C. Cummings.
1972. A 50-dB increase in sustained ambient noise from fish (*Cynoscion xanthulus*). J. Acoust. Soc. Am. 52:1266–1270.

Goldberg, A. I., J. D. Etlinger, D. F. Goldspink, and C. Jablecki.
1975. Mechanism of work-induced hypertrophy of skeletal muscle. Med. Sci. Sport. 7:248–261.

Gray, G.-A., and H. E. Winn.
1961. Reproductive ecology and sound production of the toadfish, *Opsanus tau*. Ecology 42:274–282.

Guest, W. C., and J. L. Lasswell.
1978. A note on courtship behavior and sound production of red drum. Copeia 1978:337–338.

Hawkins, A. D., and C. J. Chapman.
1966. Underwater sounds of the haddock, *Melanogrammus aeglefinus*. J. Mar. Biol. Assoc. U.K. 46:241–247.

Hawkins, A. D., and K. J. Rasmussen.
1978. The calls of gadoid fish. J. Mar. Biol. Assoc. U.K. 58:891–911.

Hildebrand, S. F., and W. C. Schroeder.
1928. Fishes of the Chesapeake Bay. Fish. Bull. 43:1–366.

Hill, G. L., M. L. Fine, and J. A. Musick.
1987. Ontogeny of the sexually dimorphic sonic muscle in three sciaenid species. Copeia 1987: 708–713.

Holloszy, J. O.
1967. Biochemical adaptations in muscle: effects of exercise on mitochondrial oxygen uptake and respiratory enzyme activity in skeletal muscle. J. Biol. Chem. 242:2278–2282.

Horch, K., and M. Salmon.
1973. Adaptations to the acoustic environment by the squirrelfishes, *Myripristis violaceus* and *M. pralinius*. Mar. Behav. Physiol. 2:121–139.

Hourigan, T. F., M. Nakamura, Y. Nagahama, K. Yamauchi, and E. G. Grau.
1991. Histology, ultrastructure and in vitro steroidogenesis of the testes of two male phenotypes of the protogynous fish, *Thalassoma duperrey* (Labridae). Gen. Comp. Endocrinol. 83:193–217.

Lamb, D. R.
1975. Androgens and exercise. Med. Sci. Sport. 7:1–5.

Lobel, P. S.
1992. Sounds produced by spawning fishes. Env. Biol. Fish. 33:351–358.

Mercer, L. P.
1983. A biological and fisheries profile of weakfish, *Cynoscion regalis*. N.C. Dep. Nat. Resour. Comm. Dev., Div. Mar. Fish. Spec. Sci. Rep. 39, 107 p.

Merriner, J. V.
1976. Aspects of the reproductive biology of the weakfish, *Cynoscion regalis* (Sciaenidae), in North Carolina. Fish. Bull. 74:18–26.

Mok, H. K., and R. G. Gilmore.
1983. Analysis of sound production in estuarine aggregations of *Pogonias cromis*, *Bairdiella chrysoura*, and *Cynoscion nebulosus* (Sciaenidae). Bull. Inst. of Zoology, Acad. Sin. 22: 157–186.

Moulton, J. M.
1956. Influencing the calling of sea robins (*Prionotus* spp.) with sound. Biol. Bull. 111:393–398.

Musacchia, X. J., J. M. Steffen, and R. D. Fell.
1988. Disuse atrophy of skeletal muscle: animal models. Exercise Sport Sci. Rev. 16:61–87.

Obert, H.-J.
1977. Hormonal influences on calling and reproductive behavior in anurans. *In* D. H. Taylor and S. I. Guttmann (eds.), The reproductive biology of amphibians, p. 357–366. Plenum Press, New York.

Ono, R. D., and S.G. Poss.
1982. Structure and innervation of the swim bladder musculature in the weakfish, *Cynoscion regalis* (Teleostei: Sciaenidae). Can. J. Zool. 60:1955–1967.

Pearson, J. C.
1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. Fish. Bull. 44:129–214.

Sassoon, D., and D. B. Kelley.
1986. The sexually dimorphic larynx of *Xenopus laevis*: development and androgen regulation. Am. J. Anat. 177:457–472.

Saucier, M. H., and D. M. Baltz.
1993. Spawning site selection by spotted seatrout, *Cynoscion nebulosus*, and black drum, *Pogonias cromis*, in Louisiana. Env. Biol. Fish. 36:257–272.

Smith, H. M.
1905. The drumming of the drum-fishes (Sciaenidae). Science 22:376–378.

Steinberg, J. C., W. C. Cummings, B. D. Brahy, and J. Y. MacBain (Spires).
1965. Further bio-acoustic studies off the west coast of North Bimini, Bahamas. Bull. Mar. Sci. 15:942–963.

Takemura, A., T. Takita, and K. Mizue.
1978. Studies on the underwater sound—VII. Underwater calls of the Japanese marine drum fishes (Sciaenidae). Bull. Jpn. Soc. Sci. Fish. 44:121–125.

Tavolga, W. N.
1958a. The significance of underwater sounds produced by males of the gobiid fish, *Bathygobius soporator*. Physiol. Zool. 31:259–271.
1958b. Underwater sounds produced by males of the blenniid fish, *Chasmodes bosquianus*. Ecology 39:759–760.
1964. Sonic characteristics and mechanisms in marine fishes. *In* W. N. Tavolga (ed.), Marine bio-acoustics, Vol. 1, p. 195–211. Pergamon Press, New York.

Templeman, W., and V. M. Hodder.
1958. Variation with fish length, sex, stage of sexual maturity, and season in the appearance and volume of the drumming muscles of the swim-bladder in the haddock, *Melanogrammus aeglefinus* (L.). J. Fish. Res. Board Can. 15:355–390.

Tower, R. W.
1908. The production of sound in the drumfishes, the sea-robin and the toadfish. Ann. NY Acad. Sci. 18:149–180.

Villoso, E. P.
1989. Reproductive biology and environmental control of spawning cycle of weakfish, *Cynoscion regalis* (Bloch and Schneider), in Delaware Bay. Ph.D. diss., Univ. Delaware, Newark, 295 p.

Welsh, W. W., and C. M. Breder Jr.
1923. Contributions to life histories of Sciaenidae of the eastern United States coast. Fish. Bull. 39:141–201.

Woods, L. C., III, and C. V. Sullivan.
1993. Reproduction of striped bass, *Morone saxatilis* (Walbaum), broodstock: monitoring maturation and hormonal induction of spawning. Aquat. Fish. Manage. 24:213–224.

Sea otter, *Enhydra lutris*, prey composition and foraging success in the northern Kodiak Archipelago

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Abstract.—During 1987 and 1988, sea otter, *Enhydra lutris*, prey composition and foraging success were studied by observing foraging otters in the northern Kodiak Archipelago. Study areas differed in the number of years in which they were occupied by sea otters and were categorized as established (occupied >25 years), intermediate (occupied 5–15 years), and frontal (occupied <5 years). Clams were the most frequently identified sea otter prey (57–67%) in all study areas, and of the clams identified to species, *Saxidomus giganteus* was the most frequently observed. Mussels, *Mytilus* spp., crabs (primarily *Telmessus* spp.), and green sea urchins, *Strongylocentrotus droebachiensis*, contributed ≤25% to the total prey within each study area. Adults did not differ in the proportion of clams, mussels, or crabs captured as prey among study areas. Adults captured clams with a greater frequency and mussels with lesser frequency than did juvenile sea otters for all study areas combined. Forage success did not differ among study areas for adults nor between adults and juveniles for all study areas combined. Adult sea otters in the established area appear to have compensated for reduced prey size by retrieving more prey items per dive; however, they obtained less clam biomass per dive than otters in the intermediate and frontal areas.

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The Kodiak Archipelago in south-central Alaska (Fig. 1) supported an abundant sea otter, *Enhydra lutris*, population prior to their commercial exploitation during the 18th and 19th centuries (Lensink, 1962; Kenyon, 1969). Following this period of unregulated harvesting of sea otters, which was terminated in 1911 (Kenyon, 1969), an isolated remnant population of sea otters remained at the northern tip of Shuyak Island (Schneider[1]). During the late 1950's through mid 1980's, episodic range expansion occurred throughout the northern Kodiak Archipelago (Lensink, 1962; Schneider[1]; Simon-Jackson et al.[2,3]).

In the absence of sea otters, dense populations of clams, crabs, sea urchins, and abalones may develop. As sea otters recolonize former habitat, shellfish densities decrease owing to sea otter predation, sometimes in combination with commercial and subsistence shellfish harvest (Garshelis et al., 1986). Sea otters have been implicated in closure of commercial and recreational fisheries in California for abalone, *Haliotis* spp. (Estes and VanBlaricom, 1985) and pismo clams, *Tivela stultorum*, (Stephenson, 1977; Miller et al.[4]). In Alaska, sea otters impacted the recreational and commercial fisheries for Dungeness crab, *Cancer magister*, in Prince William Sound (Garshelis, 1983; Garshelis et al., 1986; Kimker[5]).

During 1987–1988 the sea otter range continued to expand near southeastern Afognak Island of the Kodiak Archipelago. The natural recolonization pattern of the archipelago provided an opportunity to study the effects of sea otters on

[1] Schneider, K. B. 1976. Assessment of the distribution and abundance of sea otters along the Kenai Peninsula, Kamishak Bay and the Kodiak Archipelago. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 37:527–626.

[2] Simon-Jackson, T., D. Taylor, S. Schliebe and M. Vivion. 1985. Sea otter survey, Kodiak Island–1984. U.S. Fish and Wildlife Service, Anchorage, Alaska. Unpubl. rep., 16 p.

[3] Simon-Jackson, T., M. Vivion, and D. Zwiefelfofer. 1986. Sea otter survey, Kodiak Island–1985. U.S. Fish and Wildlife Service, Anchorage, Alaska. Unpubl. rep., 11 p.

[4] Miller, D. J., J. E. Hardwick, and W. A. Dahlstrom. 1975. Pismo clams and sea otters. Calif. Dep. Fish and Game. Mar. Resources Tech. Rep. 31:1–49.

[5] Kimker, A. 1985. A recent history of the Orca Inlet, Prince William Sound Dungeness crab fishery with specific reference to sea otter predation. *In* B. R. Metleff (ed.), Symposium on Dungeness crab biology and management, p. 231–241. Univ. of Alaska, Alaska Sea Grant Rep. 85-3.

prey populations (Kvitek et al., 1992) and an opportunity to assess changes in sea otter foraging characteristics (prey composition, forage success, prey size and biomass) as they relate to the duration the habitat had been occupied. We describe the foraging characteristics of sea otters in relation to the length of habitat occupancy along the Kodiak Archipelago.

Methods

Study area

Study areas in the Kodiak Archipelago were chosen in regions that differed in the number of years since sea otters had reoccupied the habitat (Fig. 1). We categorized the areas following Kvitek et al. (1992) as established (occupied for >25 years), intermediate (occupied for 5–15 years), and frontal (occupied for <5 years) based on sea otter surveys (Lensink, 1962; Kenyon, 1969; Schneider[1]; Simon-Jackson[2,3]; and interviews with local inhabitants). Established study sites were on southern Shuyak and northern Afognak islands, intermediate study sites were located between southern Afognak and northern Kodiak islands, and frontal study sites were southeast of Afognak and Raspberry islands. Study sites had broad expanses of shallow water (<20 m) with primarily sand and gravel sediments supporting infaunal bivalve assemblages (Kvitek et al., 1992).

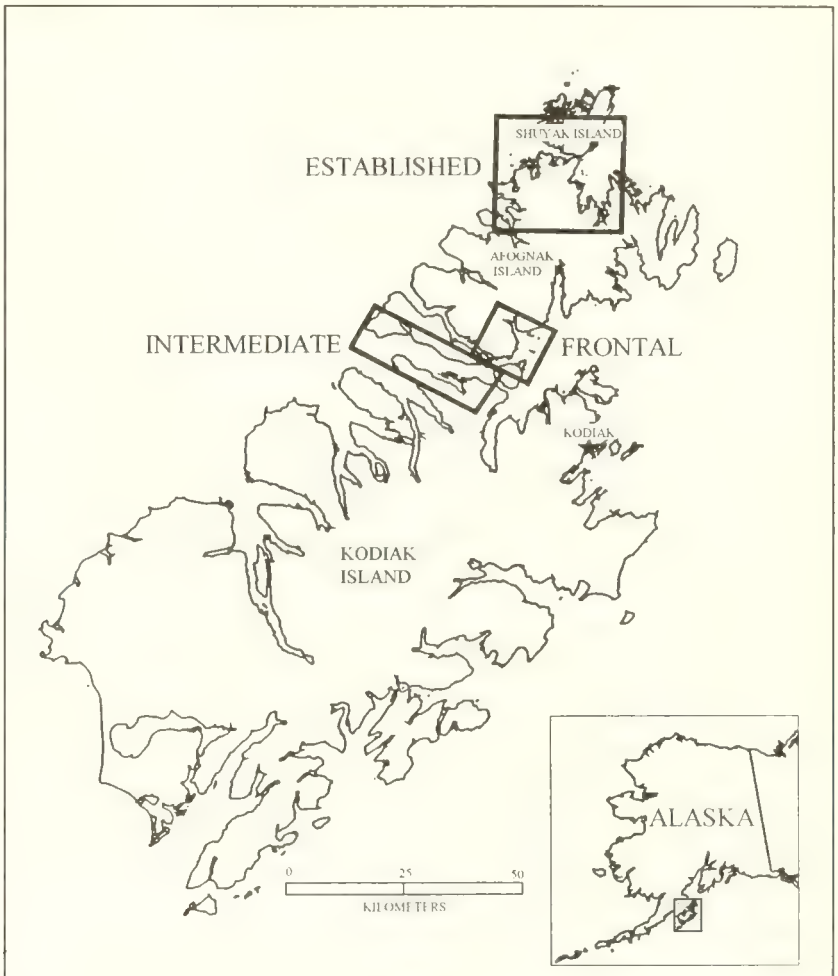

Figure 1

Study areas for observations of foraging sea otters, *Enhydra lutris*, in established (occupied >25 yr), intermediate (occupied 5–15 yr) and frontal (occupied <5 yr) areas during 1987 and 1988 in the Kodiak Archipelago, Alaska.

Foraging observations

Observations of foraging sea otters were made from shore with the aid of 10× binoculars and 40–80× telescopes (Questar Corp., New Hope, PA). Foraging data were collected by focal animal sampling (Altmann, 1974). Repeated dives were recorded for a focal animal while the animal remained in view and continued to forage (Calkins, 1978). All observations were made on unmarked animals that were within approximately 1 km of shore. Data were collected during June–October 1987 and during March, June, and September of 1988 during daylight hours and during various tidal states.

Data for each recorded dive included sex and age class of otter, presence of a pup, number of prey items obtained, identification of prey (classified to lowest possible taxon), and categorization of prey size (small <5 cm, medium 5–9 cm, and large >9 cm). Size class of prey was estimated relative to the mean forepaw width (4.5 cm) and mean skull width (10 cm) for adult sea otters (Johnson[6]). Adult otters were classified as male, female, female with pup, or unknown sex. Juveniles that were estimated to be <2 years of age were differentiated from adults by their small body size (estimated to be <18 kg) and dark pelage. Forage data on pups still associated with their mother were not collected. Forage dives were classified as successful (prey captured), unsuccessful (no prey captured), or of unknown success (observer could not determine if prey were captured).

[6] Johnson, A. M. 1987. Sea otters of Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Alaska Fish and Wildlife Research Center, Anchorage, Alaska. Unpubl. rep., 87 p.

Data partitioning

A forage record was defined as the forage data specific to a focal animal and was used as the sample unit in comparisons of prey composition, forage success, and the mean number of prey captured per dive. For assessing variation in prey composition and forage success, only forage records containing ≥10 forage dives were used; adults of unknown sex were deleted in comparisons of sex classes. Sample sizes for juveniles were small and created an unbalanced sample design in 2-way comparisons. Consequently, separate tests were conducted to assess age-class differences.

For comparisons of prey composition, we calculated the proportion of dives resulting in the capture of clams, crabs, and mussels for each forage record. Differences in the proportion of prey items captured by adult sea otters were tested among areas. Sample sizes were insufficient to test prey composition differences among areas for juveniles. Data were pooled from all study areas and the proportion of prey captured was tested by age class.

Forage success (the proportion of successful dives) was normalized by an arcsine transformation of the square root. Differences in forage success among study areas and among adult sex classes (male, female, and females with pups) were tested. Sample sizes were insufficient to test for differences among study areas for juveniles. Data were pooled for all juveniles and all adults to test age differences in forage success.

Number of prey items captured per dive was calculated by dividing the total number of prey captured by the number of forage dives per foraging record and averaging these values by sex class and area. Dives resulting in the capture of mussels (which may be difficult to count) and dives of unknown result were excluded.

We assumed mean shell lengths of 4.0, 7.0, and 10.0 cm were representative of small, medium, and large bivalve size classes, then estimated mean wet-tissue mass of *Saxidomus giganteus* by using the weight-length relationships generated by Kvitek et al. (1992). We estimated caloric gain per dive by using caloric values for this genus reported by Kenyon (1969).

Data analysis

Kruskal-Wallis nonparametric (1-way) tests were used to assess differences in the proportion of clams, mussels, and crabs captured among study areas by adult sea otters; data were pooled for all study areas and the proportion of clams, mussels, and crabs were tested by age class. Analysis of variance (2-way ANOVA) was used to test 1) differences in forage success among study areas and adult sex classes, and 2) differences in the mean number of prey captured per forage dive among study areas and adult sex classes. A 1-way ANOVA was used to test differences in the mean number of prey captured per dive among study areas for juvenile sea otters. A Student's t-test was used to test differences in forage success between adult and juvenile sea otters for all study areas combined. For all comparisons, significance was set at α=0.05.

Results

Sea otters were observed foraging on clams (57–67%), mussels (19–25%), crabs (2–4%) and green sea urchins, *Strongylocentrotus droebachiensis* (0–3%) (Fig. 2). Clams were identified to species in 23% (n=535), 65% (n=957), and 63% (n=1,060) of the observations in established, intermediate, and frontal areas, respectively. The majority of clams identified were *Saxidomus* in established (98%), intermediate (89%), and frontal (96%) areas. Other clams identified (<10% per study area) were *Tresus capax*, *Mya* spp., *Protothaca staminea*, and *Entodesma macroschisma*. *Mytilus* spp. was the most common mussel observed within the study areas. Crabs were primarily *Telmessus* spp.; however, a small number of *Cancer magister*, were recorded. Other prey which contributed from <1 to 7% of the diet in each study area included *Clinocardium* spp., *Cucumaria fallax*, *Echiurus echiurus alaskensis*, *Nucella* spp., *Octopus* spp., *Pisaster* spp., *Pycnopodia helianthoides*, barnacle (class Crustacea), chiton (class Polyplacophora), tunicate

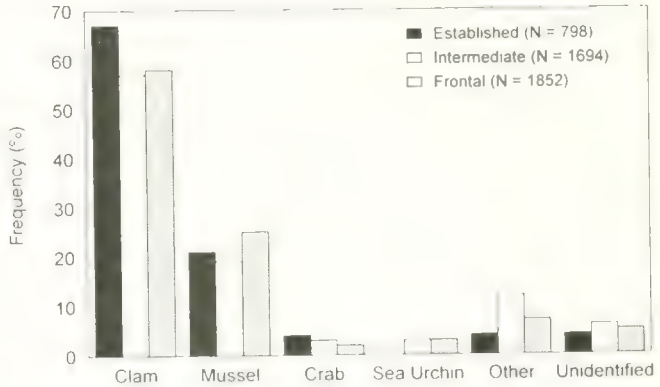

Figure 2

Frequency of occurrence of food items obtained by sea otters, *Enhydra lutris*, as determined by visual observation along the Kodiak Archipelago during 1987 and 1988 in areas of established (>25 yr), intermediate (5–15 yr), and frontal (<5 yr) sea otter forage areas.

(class Ascidiacea), and kelp (primarily kelp hold-fasts with small unidentified invertebrates attached). Unidentified prey constituted 4–6% of prey per area.

The proportion of forage dives resulting in the capture of clams, mussels, and crabs did not differ among study areas for adults. For all study areas combined, adult and juvenile sea otters differed in the proportion of forage dives capturing clams (χ^2=13.35, df=1, P<0.001) and mussels (χ^2=10.40, df=1, P=0.001) but not crabs (χ^2=3.22, df=1, P=0.07). The median proportion of dives resulting in the capture of clams ranged among study areas from 0.62 to 0.85 for adults and from 0.00 to 0.52 for juveniles. Conversely, median values for mussels ranged from 0.00 to 0.93 for juveniles and was zero for adults. Crabs were captured infrequently and the median proportion of dives capturing crabs was zero for both age classes.

Forage success did not differ among study areas (F=0.52, df=2, P=0.59) nor among sex classes (F=2.22, df=2, P=0.12) within areas for adults; the interaction between sex class and area was not significant (F=0.50, df=4, P=0.74). Mean forage success for all study areas combined was 89% for adults and 90% for juveniles and did not differ significantly (t=–0.59, df=107, P=0.56) (Table 1).

Mean number of prey captured per dive by adults in established, intermediate, and frontal areas differed among areas (1.6±1.0, 1.1±0.4, and 1.2±0.8, respectively) (F=3.88, df=2, P=0.02) but not among sex class (F=0.98, df=2, P=0.38); the interaction between sex class and area was not significant (F=1.00, df=4, P=0.41). Juvenile sea otters, did not differ in the mean number of prey captured per dive among study areas (F=0.55, df=2, P=0.59) (Table 1).

In the established area, 92% (n=526) of the clams captured by sea otters were small (<5 cm), and 8% were medium (5–9 cm). In intermediate and frontal areas, however, only 27% (n=943) and 38% (n=1,039) of all clams captured were small and the majority were medium sized. The mean caloric content of *Saxidomus* captured by adult otters per forage dive in established, intermediate, and frontal areas was estimated to be 10 kcal, 21 kcal, and 21 kcal, respectively (Table 2).

Discussion

The composition of the diet was similar for sea otters in the Kodiak Archipelago among forage areas

Table 1

Summary of foraging success and mean number of prey items per dive for juvenile and adult sea otters, *Enhydra lutris*, along the Kodiak Archipelago in established (occupied >25 years), intermediate (occupied 5–15 years), and frontal (occupied <5 years) areas.

Study area	Age and sex	No. of forage records	No. of dives	Mean % successful dives	Mean no. prey items per dive [1] ± SD
Established	Juvenile	3	30	83	1.0 ± 0.5
	Adult male	6	59	83	1.3 ± 0.8
	Adult female	4	63	96	2.1 ± 1.4
	Adult female w/pup	12	136	97	1.8 ± 0.9
	Adult unknown	9	93	97	1.4 ± 0.3
	Total	34	381		
Intermediate	Juvenile	16	223	93	1.0 ± 0.6
	Adult male	19	239	89	1.1 ± 0.6
	Adult female	27	343	78	1.0 ± 0.4
	Adult female w/pup	28	349	93	1.2 ± 0.4
	Adult unknown	8	92	86	1.1 ± 0.4
	Total	98	1,246		
Frontal	Juvenile	13	146	88	1.2 ± 0.6
	Adult male	25	296	96	1.4 ± 1.3
	Adult female	24	369	86	1.1 ± 0.4
	Adult female w/pup	14	272	96	1.3 ± 0.7
	Adult unknown	4	69	84	1.0 ± 0.03
	Total	80	1,152		

[1] Dives resulting in the capture of mussels, *Mytilus* spp., and dives of unknown result were not used in calculating mean number of prey per dive.

Table 2

Frequency and estimated biomass of *Saxidomus giganteus* retrieved per dive by adult sea otters, *Enhydra lutris*, in established (occupied for >25 years), intermediate (occupied 5–15 years), and frontal (occupied <5 years) study areas along the Kodiak Archipelago, Alaska, 1987–1988.

Study area	Size class (mm)	Proportion in sample	Mean number of prey/dive	Estimated wet-tissue weight obtained/dive (g) [1]	Estimated caloric content (kcal)
Established	<50	0.83	1.6	16	10
	50–90	0.17			
Intermediate	<50	0.18	1.1	33	21
	50–90	0.71			
	>90	0.11			
Frontal	<50	0.28	1.2	33	21
	50–90	0.62			
	>90	0.10			

[1] Wet-tissue weight=2.14 (10^{-4})(shell length)$^{2.78}$; r^2=0.86 for *Saxidomus giganteus* where shell lengths equal 40, 70, and 100 mm representing small, medium, and large size classes, respectively (Kvitek et al., 1992).

irrespective of the number of years the habitat had been occupied by sea otters. Clams, particularly *Saxidomus*, were the predominant prey identified in all study areas, although 35–77% of the clams were not identified to species. Green sea urchins were absent in the diets of sea otters in established areas but were found, infrequently, in the prey composition in intermediate and frontal areas. Sea urchins were apparently locally abundant in intermediate and frontal areas prior to the initiation of our study (Kvitek et al., 1992; Stanford and Cunningham[7]). Sea urchin abundance had been reduced to low levels by sea otter predation in other regions of Alaska and in California (Lowry and Pearse, 1973; Estes et al., 1978; Laur et al., 1988; Kvitek et al., 1989) and it is likely that sea otter predation affected urchin populations in the Kodiak Archipelago.

Juvenile sea otter diets contained a higher proportion of mussels than that of adults. A higher occurrence of mussels in the diet of juveniles than of adult sea otters has also been demonstrated by other studies conducted in Alaska (VanBlaricom, 1988; Doroff and Bodkin, in press; Johnson[6]). Mussels are an easily obtainable intertidal prey, and young sea otters may rely on mussels as a food source until they become more proficient foragers (Estes et al., 1981; VanBlaricom, 1988).

Sea otters at Kodiak were highly successful in securing prey, even where prey had been reduced by years of otter predation (Kvitek et al., 1992). Therefore, forage success was not a useful criterion for discriminating among study areas that varied in the duration of sea otter occupancy. For sea otters, forage success may vary with prey type, hunting tactics, or locality (Ostfeld, 1991) and may not be related to prey abundance or biomass (Estes et al., 1981). Ostfeld (1991) suggested, however, that forage success is a useful means of comparing forage strategies and habitat characteristics for sea otters. The lack of variation in forage success among our study areas may have resulted, in part, from similarities in habitat (Kvitek et al., 1992). Kruuk et al. (1990) recommended caution in defining and using the concept of forage success on a per dive basis and suggested that a more meaningful approach would be to examine the biomass captured per unit of effort.

We estimated the average biomass and subsequent caloric value captured on a per dive basis for sea otters. Sea otters foraging in habitat occupied an estimated 1–15 years obtained approximately twice the biomass of otters foraging in habitat occupied >25 years. This suggests that sea otters foraging in long-occupied habitat may need to compensate for reduced prey size and abundance through increased allocation of time for foraging to meet minimum daily caloric requirements (Costa, 1978; Estes et al., 1982; Estes et al., 1986; Garshelis et al., 1986). Biomass and caloric values were similar for intermediate and frontal areas. Possible explanations for the lack of disparity between intermediate and frontal areas are 1) preexisting habitat differences among study areas, 2) resilience of *Saxidomus* to sea otter predation over the short term (see Kvitek et al., 1988), or 3) an error in the classification of study areas.

We made the assumption that observed differences in foraging characteristics resulted primarily from

Stanford, S., and W. Cunningham. Bare Island, Port Bailey, AK 99615. Personal commun., June 1987.

sea otter predation. There were likely preexisting differences in the community structure among our study areas that were not assessed, such as the distribution and abundance of bivalve species prior to sea otters re-occupying the study areas. However, we believe that comparisons of study areas are valid given the similarities in habitat and infaunal invertebrate assemblages among study areas documented by Kvitek et al. (1992).

Saxidomus may appear resilient to sea otter predation pressure over the short term because it is present in high densities in our study areas (Kvitek et al., 1992). *Saxidomus* was found in higher densities than was any other forage species and it was selected preferentially (based on differences between in situ population of clams and the shells discarded by foraging otters) in intermediate and frontal areas (Kvitek et al., 1992). *Saxidomus* was also the most abundant clam (in situ) in the established area; however, *Protothaca* was selected preferentially (Kvitek et al., 1992). *Protothaca* was not identified visually as sea otter prey in the established area; however, only 23% of the clams could be identified to species.

We believe the classification of our study areas and those used by Kvitek et al. (1992) were correct; however, our methods lacked the refinement needed to distinguish between intermediate and frontal areas. Kvitek et al. (1992) was also unable to detect differences between the intermediate and frontal areas by measuring prey size directly from the shells of clams consumed by sea otters. However, there were differences in the size of the in situ population of clams between areas (Kvitek et al., 1992). Newly exploited habitat in our study was represented by an area estimated to have been occupied 1–4 years by sea otters. Rapid changes may occur within the first year that sea otters occupy unexploited habitat. Garshelis et al. (1986) observed an approximate twofold decrease in kcal/dive in areas occupied by sea otters ≤1 year compared with areas occupied 1–2 years. Coincident with the change in kcal/dive was a shift in prey from crabs to clams between areas studied by Garshelis et al. (1986). In the Kodiak Archipelago, we did not observe differences in mean kcal/dive or changes in prey composition between intermediate and frontal areas. Changes in prey composition, such as the potential removal of green sea urchins from the study area, may have occurred in the frontal area during the first year and were undetected.

Adult sea otters in the established area appear to have compensated for reduced prey size by retrieving more prey items per dive. However, they still obtained less clam biomass (and subsequently less caloric intake) per dive than otters in the intermediate and frontal areas, suggesting that they may need to forage longer to meet minimum daily caloric needs. Interestingly, juveniles in established areas did not appear to compensate for reduced bivalve prey size by increasing the number of prey captured per dive. Juveniles may be less efficient foragers and may compensate by increasing their consumption of *Mytilus* spp., which are an easily obtainable intertidal prey (Estes, 1981; VanBlaricom, 1988; Doroff and Bodkin, in press).

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Literature cited

Altmann, J.
1974. Observational study of behavior: sampling methods. Behavior 49:227–267.

Calkins, D. G.
1978. Feeding behavior and major prey species of the sea otter, *Enhydra lutris*, in Montague Strait, Prince William Sound, Alaska. Fish. Bull. 76:125–131.

Costa, D. P.
1978. The ecological energetics, water, and electrolyte balance of the California sea otter, *Enhydra lutris*. Ph.D. diss., Univ. California, Santa Cruz, 75 p.

Doroff, A. M., and J. L. Bodkin.
In press. Sea otter foraging behavior and hydrocarbon levels in prey. *In* T. R. Loughlin (ed.), Impacts of the *Exxon Valdez* oil spill on marine mammals. Academic Press.

Estes, J. A., and G. R. VanBlaricom.
1985. Sea otters and shellfisheries. *In* R. Beverton, J. Beddington, and D. Lavigne (eds.), Conflicts between marine mammals and fisheries, p. 187–235. Allen and Unwin, London, England.

Estes, J. A., N. S. Smith, and J. F. Palmisano.
1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. Ecology 59:822–833.

Estes, J. A., R. J. Jameson, and A. M. Johnson.
1981. Food selection and some foraging tactics of sea otter. *In* J. A. Chapman and D. Pursley (eds.), The worldwide furbearer conference proceedings, p. 606–641. Worldwide Furbearers Conf., Inc., Frostburg, MD.

Estes, J. A., R. J. Jameson, and E. B. Rhode.
1982. Activity and prey selection in the sea otter: influence of population status on community structure. Am. Nat. 120:242–258.

Estes, J. A. , K. Underwood, and M. Karmann.
1986. Activity time budgets of sea otters in California. J. Wildl. Manage. 50:626–639.

Garshelis, D. L.
1983. Ecology of sea otters in Prince William Sound, Alaska. Ph.D. diss., Univ. Minnesota, MN, 321 p.

Garshelis, D. L., J. A. Garshelis, and A. T. Kimker.
1986. Sea otter time budgets and prey relationships in Alaska. J. Wildl. Manage. 50(4):637–647.

Kenyon, K. W.
1969. The sea otter in the eastern Pacific Ocean. North Am. Fauna. 68:1–352.

Kruuk, H., D. Wansink, and A. Moorhouse.
1990. Feeding patches and diving success of otters, *Lutra lutra*, in Shetland. Oikos 57:68–72.

Kvitek, R. G., A. K. Fukuyama, B. S. Anderson, and B. K. Grimm.
1988. Sea otter foraging on deep-burrowing bivalves in a California coastal lagoon. Mar. Biol. 98:157–167.

Kvitek, R. G., D. Shull, D. Canestro, E. C. Bowlby, and B. L. Troutman.
1989. Sea otters and benthic prey communities in Washington State. Mar. Mamm. Sci. 5(3):226–280.

Kvitek, R. G., J. S. Oliver, A. R. DeGange, and B. S. Anderson.
1992. Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. Ecology 73(2):413–428.

Laur, D. R., A. W. Ebeling, and D. A. Coon.
1988. Effects of sea otter foraging on subtidal reef communities off central California. *In* G. R. VanBlaricom and J. A. Estes (eds.), The community ecology of sea otters, p. 159–168. Springer-Verlag, Berlin, West Germany.

Lensink, C. J.
1962. The history and status of sea otters in Alaska. Ph.D. diss., Purdue Univ., West LaFayette, IN, 188 p.

Lowry, L. F., and J. S. Pearse.
1973. Abalones and sea urchins in an area inhabited by sea otters. Mar. Biol. 23:213–219.

Ostfeld, R. S.
1991. Measuring diving success of otters. Oikos 60:258–260.

Stephenson, M. D.
1977. Sea otter predation an Pismo clams in Monterey Bay. Calif. Fish Game 63:117–120.

VanBlaricom, G. R.
1988. Effects of foraging by sea otters on mussel-dominated intertidal communities. *In* G. R. VanBlaricom and J. A. Estes (eds.), The community ecology of sea otters, p. 48–91. Springer-Verlag, Berlin, West Germany.

Abstract.—We developed a relatively simple and parsimonious (SMPAR) biomass dynamics model for estimating abundance of northern anchovy, *Engraulis mordax*, off southern California and Baja California, Mexico, during the 1963 to 1991 fishing seasons. The SMPAR model was a compromise between simple surplus production and complex age-structured models. It was designed to give more precise biomass estimates for management of northern anchovy for which there are no age-composition data and only noisy abundance index data. We evaluated consistent bias in biomass and recruitment estimates, bias in recruitment estimates due to log transformation, and retrospective bias. Simple corrections based on bootstrap procedures were used to remove consistent bias and log transformation bias. Retrospective bias was not a significant problem. Results indicate that the SMPAR model estimates stock biomass more reliably than recruitment because abundance indices for northern anchovy contain little information about interannual recruitment variability. Asymptotic variance estimates calculated by inverting the Hessian matrix averaged 20% smaller than variances calculated by bootstrapping. Outliers in abundance data were the biggest source of uncertainty in biomass estimates. Simulation results indicate that our approach could be useful in a variety of situations.

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A biomass-based assessment model for northern anchovy, *Engraulis mordax*

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Northern anchovy, *Engraulis mordax*, is a small (<18 cm TL), short lived (<8 years) pelagic schooling fish (Baxter, 1967). The central stock of northern anchovy extends from Mexico to central California (lat. 30°–35°N); most of the stock inhabits the Southern California Bight. Spawning occurs all year with a peak between February and April (MacCall and Prager, 1988).

The central stock of northern anchovy is among the world's most thoroughly studied fish stocks. Reliable estimates of northern anchovy biomass were not available, however, until the daily egg production method was used to estimate spawning biomass from 1980 to 1985 (Lasker, 1985). Estimates of long-term trends in biomass were not available until the stock synthesis model for northern anchovy was developed (Methot, 1989). The stock synthesis model was used to manage northern anchovy until 1992 after availability of age-composition data declined.[1]

As data became limited, variance and bias of biomass estimates[2] from the stock synthesis model increased. Bias problems included a positive "retrospective" bias in recent estimates and a smaller but consistent positive bias in estimates for earlier seasons (Lo et al., 1992). Retrospective bias is a newly recognized but common problem in fish stock assessment work (Sinclair et al., 1991) that makes recent biomass estimates too large. Consistent bias (usually positive) is a problem of variable severity in biomass estimates from most assessment models including the stock synthesis model (Lo et al., 1992; Bence et al., 1993), derivatives[3] of CAGEAN (Deriso et al., 1985), and virtual population analysis or VPA (e.g. Lapointe et al., 1989). Consistent bias, unlike retrospective bias, affects all or most of the biomass estimates from a model.

We hypothesized that problems in the stock synthesis model for north-

[1] Jacobson, L. D., and N. C. H. Lo. 1992. Spawning biomass of the northern anchovy in 1992. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-92-24, 71 p.

[2] Jacobson, L. D., and N. C. H. Lo. 1991. Spawning biomass of the northern anchovy in 1991. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-91-19, 53 p.

[3] Deriso, R. 1993. A report on integrated stock assessment of Pacific sardine, Appendix 2. *In* F. J. Hester, Project report on Pacific sardine (*Sardinops sagax*) resource research, 1991/1992 phase III. Living Marine Resources Inc., 11855 Sorrento Valley Road, Suite A, San Diego, CA 92121. Final Rep. to Calif. Seafood Council, P.O. Box 91540, Santa Barbara, CA 93190, 118 p.

ern anchovy were exacerbated by use of a complicated model with insufficient data. The model we developed for northern anchovy was, therefore, simpler and more parsimonious (SMPAR).

The SMPAR model is a biomass dynamic model designed to give more precise biomass estimates for management of northern anchovy. SMPAR is a hybrid between simple surplus production and complex age-structured models. It resembles a surplus production model because age-composition data are not used and fishing mortality rates are equal for all age groups. The model is age structured, however, and some rudimentary relationships between age-specific abundance and abundance indices are assumed.

As described above, the SMPAR model for northern anchovy did not use any age-composition data, although data were available for most fishing seasons prior to 1991. We chose to exclude age-composition data from our model because the data are difficult to interpret, require complex modeling approaches, and were not available for recent seasons.

In this paper, we describe the SMPAR model and data for northern anchovy. Bias and variance in biomass and recruitment estimates are assessed by using bootstrap techniques. Sensitivity analyses show how model assumptions and contradictory trends in the data affect biomass estimates from SMPAR. We use simulation analysis to show how SMPAR would perform under a wide range of fishing mortality and recruitment conditions.

Data and methods

Fishing seasons were used to aggregate most of our data including landings data and indices of abundance (Table 1; Fig. 1). Fishing seasons for northern

Table 1

Data for northern anchovy, *Engraulis mordax*, by fishing season (1 July to 30 June): fish spotter data (SPOTTER), historical egg production data (HEP), new egg production index (EPI), sonar data (SONAR), and daily egg production method data (DEP). CV denotes coefficient of variation. Temperatures are average sea surface temperatures at Scripps Pier, San Diego, California during January and February.

Fishing season	SPOTTER (short tons·block^{-1})	CV (%)	HEP (eggs 0.05 m^{-2} day^{-1})	CV (%)	EPI (eggs 0.05 m^{-2} day^{-1})	CV (%)	SONAR	DEP (10^{12} t)	CV (%)	Mexican landings (10^{3} t)	US landings (10^{3} t)	Total landings (10^{3} t)	Temperature (°C)
1963	0.9	28	4.1	65						0.000	1.795	1.795	15.0
1964	10.5	31	4.0	29						0.000	2.324	2.324	13.3
1965	8.2	32	5.3	34						0.000	18.958	18.958	13.8
1966	11.2	30								0.000	42.725	42.725	14.0
1967	6.7	31								0.000	13.470	13.470	14.5
1968	3.9	35	3.8	28			0.44			0.000	33.224	33.224	14.3
1969	18.6	30					0.28			0.000	83.391	83.391	13.6
1970	10.2	32					0.23			0.000	81.854	81.854	13.1
1971	13.8	30	1.7	48			0.82			0.000	55.624	55.624	12.8
1972	10.3	33					1.67			0.000	76.059	76.059	15.0
1973	73.6	29					0.95			0.000	116.666	116.666	13.1
1974	42.9	29	19.7	53			3.09			28.088	113.782	141.870	13.2
1975	60.2	28								35.287	135.573	170.860	13.9
1976	34.7	31					1.98			108.962	104.095	213.057	16.0
1977	33.4	29	2.3	192			0.39			127.229	76.236	203.465	15.7
1978	49.5	34	5.4	48			0.29			195.675	55.966	251.641	13.9
1979	77.2	34	2.7	47	2.2	27	0.60	870	26	157.543	40.091	197.634	15.0
1980	42.0	38	4.4	48	3.0	14	0.57	635	22	287.547	65.906	353.453	14.6
1981	22.0	38	3.3	41	1.9	17	0.25	415	26	255.086	53.212	308.298	14.1
1982	27.3	39	3.9	30	2.2	34	0.53	652	21	156.725	11.003	167.728	15.9
1983	7.3	49	2.9	37	5.8	11	0.57	309	17	66.260	7.507	73.767	15.0
1984	25.7	45	2.6	26	6.9	48	1.02	521	19	123.359	4.762	128.121	13.8
1985	20.2	42			7.1	32				85.801	6.321	92.122	15.2
1986	8.6	43			5.0	16				116.334	4.783	121.117	15.0
1987	5.7	46			6.3	33				98.498	5.794	104.292	14.0
1988	30.5	40			1.5	29				86.361	5.795	92.156	13.0
1989	9.7	45			2.3	35				55.647	8.228	63.875	14.4
1990	5.0	55			1.8	23				0.796	10.328	11.124	14.9
1991	12.1	54			0.9	32				0.134	4.546	4.680	15.3

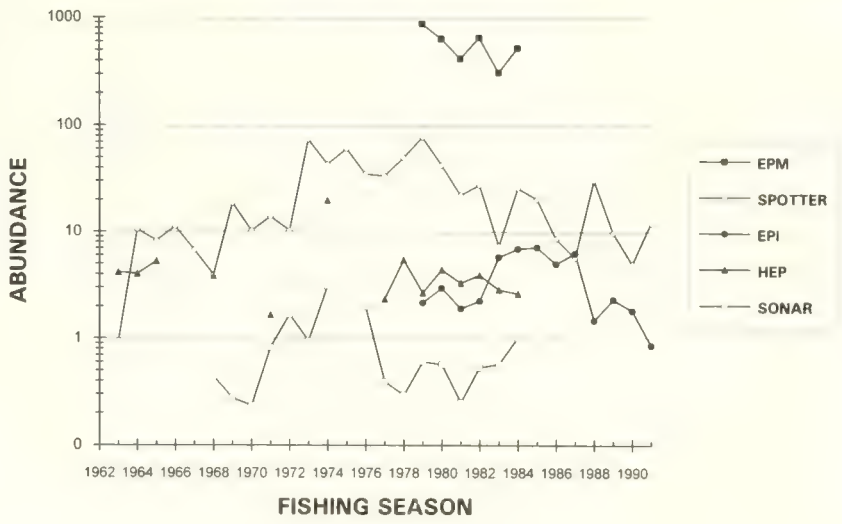

Figure 1

Indices of abundance for northern anchovy, *Engraulis mordax* (log scale). The SPOTTER index is based on fish spotter data, HEP is the historical egg production index, EPI is the new egg production index, SONAR is based on sonar data, and DEP is daily egg production method estimates of spawning biomass.

anchovy begin on 1 July, end on 30 June, and are identified by the calendar year on 1 July. We assumed that indices for northern anchovy measured abundance during the peak spawning period which is about 15 February.

Indices of abundance used to estimate northern anchovy biomass included 1) spawning biomass estimated by the daily egg production method (DEP, Gunderson, 1993; formerly called the egg production method or EPM, Lasker, 1985), 2) a historical egg production index (HEP, Lo, 1985), 3) our new egg production index (EPI), 4) relative biomass of schooled fish estimated from fish spotter data (SPOTTER, Lo et al., 1992), and 5) relative biomass of schooled fish estimated from California Department of Fish and Game sonar data (SONAR, Mais, 1974; Methot, 1989). Indices that measured relative abundance of northern anchovy (Fig. 1) were not all positively correlated and none of the correlations were statistically significant. Lack of significant correlation may have been due to relatively few years of data used to compute some correlations, to imprecise indices, and to differences among indices in area surveyed. Of particular concern is the lack of significant positive correlation between the EPI and SPOTTER indices which are the only relative abundance data available for recent fishing seasons.

Daily egg production method (DEP) estimates of spawning biomass during the 1979 to 1984 seasons (Table 1, Fig. 1) measured spawning biomass in metric tons (t), rather than in relative units, and are relatively precise (coefficients of variation (CV) less than 27%). Only six DEP observations were available, but the DEP data were important because they helped scale indices of relative abundance for northern anchovy to units of absolute biomass (Bence et al., 1993).

SONAR data did not include variances that were required in our model. We used the standard deviation (ε=0.439) of log-scale residuals for SONAR values from a previous study[2] and the relationship

$$CV = \sqrt{e^{\varepsilon^2} - 1} \quad (1)$$

to obtain a crude estimate (46%) of the arithmetic scale coefficient of variation.

The SPOTTER index used in this study (Table 1, Fig. 1) was similar to the one developed by Lo et al. (1992) except that April to March, rather than January to December, annual periods were used to aggregate data. The SPOTTER index value for the 1963 fishing season was anomalously low (Fig. 1). Following Lo et al. (1992), we excluded the 1963 value because the data collection program was new in 1963 and the information may not have been reliable.

New egg production index (EPI)

Our new egg production index (EPI) measures egg production by northern anchovy during the 1979 to

1991 fishing seasons in the reduced CalCOFI (California Cooperative Oceanic Fishery Investigation) sampling area surveyed since 1985 (Hewitt, 1988). The HEP index, in contrast, is based on a relatively large grid of CalCOFI sampling stations occupied prior to the 1985 season. As explained below, the EPI makes use of all egg and larva data and is more precise than the modified historical egg production (MHEP) index used for recent seasons by Lo and Methot (1989). Both the HEP and EPI indices of egg production for northern anchovy during the 1979 to 1984 fishing seasons were used so that the model could calibrate the HEP and EPI against each other and against DEP spawning biomass estimates.

The EPI for northern anchovy averages values obtained by using the HEP method and a single equation model (SEM) developed by Lo (1986). We refer to the HEP "method" here to distinguish between the HEP index and calculations for recent seasons based on data from the reduced CalCOFI grid.

The EPI index was computed as

$$I_{EPI,y} = W_{SEM,y} I_{SEM,y} + W_{HEP,y} I_{HEP,y}, \quad (2)$$

where the $I_{t,y}$ are indices of egg production for northern anchovy during fishing season y, and the $W_{t,y}$ are weights. Weights were derived from squared inverse coefficients of variation:

$$W_{s,y} = \frac{\frac{1}{CV_{s,y}^2}}{\frac{1}{CV_{HEP,y}^2} + \frac{1}{CV_{SEM,y}^2}}, \quad (3)$$

where $CV_{s,y}$ is the coefficient of variation for index s (either SEM or HEP) in fishing season y. Variances for the EPI index were approximated

$$VAR(I_{EPI,y}) = W_{SEM,y}^2 VAR(I_{SEM,y}) + W_{HEP,y}^2 VAR(I_{HEP,y}), \quad (4)$$

where VAR denotes variance.

The weighted EPI estimates of egg production for northern anchovy were similar to HEP method and SEM estimates but more precise (Table 2). The improvement in precision is overestimated, however, because covariance between measurement errors in SEM and HEP values in each year were not included in Equation 4.

Model

Our model for northern anchovy was based on a forward simulation approach (Hilborn and Walters, 1992) like that used in the stock synthesis model (Methot, 1989; Methot, 1990) and CAGEAN (Deriso et al., 1985). The model simulated abundance of northern anchovy during the 1963 to 1991 fishing seasons given a set of parameter estimates, data for catches, and ocean temperatures. Parameters were estimated by maximum likelihood calculations that compared observed abundance indices with values predicted by the simulation model. Catch data for northern anchovy and temperature data were assumed to be measured without error; abundance indices were assumed to include measurement error.

Table 2

Egg production indices for northern anchovy, *Engraulis mordax*, in the reduced CalCOFI area during peak spawning (15 February): historical egg production method (HEP), single equation model (SEM), and the new weighted index (EPI). SE is standard error, CV is coefficient of variation, and "weights" are weights used in computing EPI values.

		HEP				SEM				EPI		
Calendar year	Fishing season	Eggs (0.05 m^{-1} day^{-1}	SE	CV (%)	Weights	Eggs (0.05 m^{-1} day^{-1}	SE	CV (%)	Weights	Eggs (0.05 m^{-1} day^{-1}	SE	CV (%)
1980	1979	1.49	0.49	33	0.61	3.19	1.30	41	0.39	2.16	0.59	27
1981	1980	2.20	0.37	17	0.64	4.33	0.98	23	0.36	2.96	0.42	14
1982	1981	1.16	3.42	296	0.00	1.90	0.32	17	1.00	1.90	0.32	17
1983	1982	3.18	1.72	54	0.36	1.71	0.69	40	0.64	2.24	0.76	34
1984	1983	6.12	3.57	58	0.04	5.74	0.65	11	0.96	5.75	0.64	11
1985	1984	8.13	4.43	55	0.70	3.92	3.30	84	0.30	6.89	3.27	48
1986	1985	8.23	4.48	54	0.35	6.53	2.62	40	0.65	7.13	2.32	32
1987	1986	8.98	3.18	35	0.17	4.13	0.67	16	0.83	4.97	0.78	16
1988	1987	6.58	3.41	52	0.40	6.05	2.54	42	0.60	6.26	2.04	33
1989	1988	0.23	0.11	46	0.30	2.01	0.61	30	0.70	1.47	0.43	29
1990	1989	2.35	0.85	36	0.91	1.89	2.24	119	0.09	2.31	0.80	35
1991	1990	2.13	1.07	50	0.20	1.74	0.44	25	0.80	1.82	0.41	23
1992	1991	0.15	0.04	29	0.61	1.98	0.71	36	0.39	0.86	0.28	32

Population dynamics

Fishing seasons were used as annual time steps, and ages 0 to 4+ were included (age group 4+ includes northern anchovy age 4 and older). Fish were aged in the model at the beginning of each fishing season on 1 July when recruitment of age-0 northern anchovy was assumed to occur (Methot, 1989). In reality, some recruitment of northern anchovy occurs throughout the year (MacCall and Prager, 1988). Therefore, our estimates of recruitment should be regarded as estimates of "effective" recruitment, i.e. biomass of age-0 fish that would have been necessary on 1 July to account for the biomass of the cohort in later years.

Numbers of northern anchovy were not included in SMPAR; abundance was measured solely in units of biomass because weight at age for northern anchovy changes rapidly throughout the year, and depends on where samples are taken (Parrish et al., 1985). In addition, weight-at-age data from commercial fisheries for northern anchovy were not available for recent fishing seasons.

Biomass dynamics were modeled as

$$B_{a+1,y+1} = B_{a,y} e^{\eta_y}, \quad (5)$$

where $B_{a,y}$ is the biomass of northern anchovy age a (a>0, i.e. excluding new recruits) at the beginning of fishing season y and η_y is the net instantaneous rate of change for northern anchovy in fishing season y. Random process errors (e.g. variation in growth and natural mortality, Hilborn and Walters, 1992) were captured in the model by recruitment estimates.

For modeling purposes, recruitment of northern anchovy in each year was assumed independent of spawning stock size:

$$B_{0,y} = \overline{B}_0 e^{\delta_y}, \quad (6)$$

where $B_{0,y}$ is recruitment (biomass age-0 fish) in fishing season y, B_0 is mean recruitment during the study period, and δ_y is a log-normally distributed error term for fishing season y with mean zero and standard deviation σ. Recruitments in each fishing season ($B_{0,y}$) were treated as parameters and estimated by the model.

The net instantaneous rate of change for northern anchovy biomass in each fishing season (η_y in Eqn. 5) is the sum of rates for fishing mortality, growth, and natural mortality:

$$\eta_y = F_y + M - G, \quad (7)$$

where F_y is the fishing mortality rate in fishing season y, M is the natural mortality rate, and G is the growth rate. All rates are defined as positive values. The fishing mortality rate for each fishing season (F_y) was assumed constant over ages but variable over time, whereas rates for natural mortality (M) and growth (G) were assumed constant over ages and time. Fishing mortality rates were calculated by using the "forward solution" algorithm in Sims (1982) and actual catch data (Table 1; Fig. 1).

The rate of natural mortality (M) for northern anchovy was assumed to be 0.8 yr^{-1}, which is reasonable for a fish that seldom exceeds seven years in age (Hoenig, 1983). Methot (1989) found that different levels of natural mortality had only modest effects on biomass estimates for northern anchovy because the estimates were anchored by DEP spawning biomass measurements.

Modeling growth as an instantaneous rate (G) is appropriate for northern anchovy because fish grow rapidly throughout the fishing season (Zhang and Sullivan, 1988). By treating growth as an instantaneous rate, northern anchovy are, in effect, allowed to continue growing in the model until they are caught.

The rate for growth used in the SMPAR model for northern anchovy (G=0.198 yr^{-1}, SE=0.0166) was estimated by fitting an exponential growth model to mean weight at age data from three sources (Methot, 1989). The exponential growth model was logarithmically transformed to give

$$\ln(W_{d,a}) = \ln(W_{d,0}) + aG, \quad (8)$$

where $W_{d,a}$ is the mean weight of northern anchovy age a in data set d, and $W_{d,0}$ is the estimated weight at age 0. The approach assumes that northern anchovy may differ in initial weight as measured by the $W_{d,0}$ parameters but experience the same rate of exponential growth (G). Parameter estimates for Equation 8 were obtained by linear regression and standard general linear model techniques (Weisberg, 1980). Residuals were dome-shaped because of the linear approximation to the asymptotic growth pattern but the linear regression model explained most of the variation in log-scale size at age (R^2=93%).

Abundance data

Abundance data (EPI, HEP, SONAR, DEP, and SPOTTER abundance indices) were assumed to be measured with log-normally distributed random errors. Predicted values for abundance data during each fishing season were calculated in the model as:

$$\hat{I}_{t,y} = Q_t \sum_{a=0}^{4+} \rho_{t,a} B_{a,y} e^{\eta_y}, \quad (9)$$

where hats (^) denote estimates, $I_{t,y}$ is the value for abundance index t in fishing season y, Q_t scales northern anchovy biomass to the units of abundance index t, and $\rho_{t,a}$ is the relative contribution of a northern anchovy at age a to abundance index t. We assumed age-specific selectivity patterns for abundance indices because estimates for most parameters were available outside of the model. This approach gave a more realistic model without increasing the number of parameters estimated. Values of $\rho_{t,a}$ were relative measures scaled to the interval [0,1], and the age with maximum relative contribution for abundance index t had $\rho_{t,a}$=1.0.

Estimates of the scaling parameter for DEP data (Q_{DEP}=1) and age-specific parameters ($\rho_{t,a}$) for DEP, HEP, and EPI data were from Methot (1989). Two-year-old northern anchovy are all sexually mature during the peak spawning period ($\rho_{DEP,2+}$=1.0), whereas the fraction of one-year-olds that are mature ($\rho_{DEP,1}$) depends on water temperatures. Maturity of age-1 northern anchovy during the peak spawning season was calculated from mean January–February sea surface temperatures at Scripps Pier, San Diego, California (Table 1), as described in Methot (1989).

Estimates of age-specific egg production for actively spawning northern anchovy (Methot, 1989) were used to estimate the age-specific parameters ($\rho_{HEP,a}$ and $\rho_{EPI,a}$) for egg production indices. No age-0 northern anchovy spawn during the peak spawning period but all are actively spawning by age 2. The fraction of actively spawning fish was also calculated from mean sea surface temperatures (Methot, 1989).

Age-specific parameters for contribution to egg production indices ($\rho_{HEP,a}$ and $\rho_{EPI,a}$) were assumed to be the product of relative egg production and fraction active. Relative egg production values were the same as those used by Methot (1989) and originally by Parrish et al. (1986).

For simplicity, relative age-specific contributions to indices of schooling biomass (SPOTTER and SONAR) for northern anchovy ages 1 and older ($\rho_{SPOTTER,1+}$ and $\rho_{SONAR,1+}$) were assumed to be 1.0. The contribution of age-0 northern anchovy to the SPOTTER and SONAR indices was estimated as

$$\rho_{SPOTTER,0} = \rho_{SONAR,0} = \frac{e^{\pi}}{1+e^{\pi}}, \tag{10}$$

where π was a parameter estimated by the model.

Objective function

Parameters in SMPAR were estimated by maximizing a function proportional to the total log-likelihood (L_{total}):

$$L_{total} \sim -\sum_{t=1}^{5} \lambda_t \sum_{y=1}^{N_t} D_{t,y}^2 - \lambda_6 \sum_{y=1}^{N_y} R_y^2, \tag{11}$$

where N_t is the number of observations for abundance index t, and N_y is the number of recruitment estimates. The λ_t values are weights that determine how important different types of data are in parameter estimation; they were set to one except during sensitivity analyses. $D_{t,y}$ is the log-scale standardized residual for abundance index t in fishing season y and R_y is the log-scale standardized residual for recruitment in fishing season y:

$$D_{t,y} = \frac{\ln(I_{t,y}/\hat{I}_{t,y})}{\varepsilon_{t,y}} = \frac{\ln(I_{t,y}) - \ln(\hat{I}_{t,y})}{\varepsilon_{t,y}}, \tag{12}$$

$$R_y = \frac{\ln(B_{0,y}/\overline{B}_0)}{\sigma} = \frac{\delta_y}{\sigma}, \tag{13}$$

where $\varepsilon_{t,y}$ is the log-scale standard error for abundance type t in fishing season y, and σ is the standard deviation for log-scale recruitment deviations (δ_y in Eqn. 6). Log-scale standard errors for abundance data ($\varepsilon_{t,y}$) were calculated from arithmetic scale coefficients of variation by inverting Equation 1.

The first term on the right side of Equation 11 gives the log likelihood of abundance indices given parameters in the model. The second term gives the log likelihood of recruitment estimates. Mean recruitment ($\overline{B}_0$ in Eqn. 13) is a "nuisance" parameter that was set equal at each iteration to the mean of current recruitment estimates. The log-scale standard deviation assumed for recruitments (σ=0.71) was calculated from stock synthesis model[2] recruitment estimates and was higher than the average standard deviation (0.48) for 41 other stocks of clupeoid fishes (Beddington and Cooke, 1983; Myers et al., 1990).

The likelihood term for recruitments in Equation 11 is a constraint that penalizes individual recruitment estimates that are different from the mean. Larger deviations and smaller σ values result in larger penalties. The constraint does not penalize serial correlation so that "runs" of good or bad recruitments can be estimated by the model. This was important because northern anchovy recruitments tend to be serially correlated (see below).

Jacobson and Lo[2] showed that a northern anchovy model without age-composition data or a recruitment

constraint like that in Equation 11 was overparameterized because recruitments need occur only once every two to three years for the model to match observed and predicted abundance data. Age-composition data for northern anchovy indicate, however, that some recruitment occurs during every fishing season (Lo and Methot, 1989). We included the recruitment constraint and a recruitment parameter for each season to obtain a more realistic model and to constrain the recruitment estimate for the last fishing season which was otherwise difficult to estimate. The constraint on recruitment biases recruitment and biomass estimates towards the mean because recruitment estimates will be high in years with poor recruitment and low in years with high recruitment.

Parameters in the model were estimated by using the simplex algorithm (Press et al., 1990). Variances and correlations for parameter and biomass estimates were calculated by using a parametric bootstrap approach (Efron, 1982) as described in Lo et al. (1992) except that simulated abundance data were generated by assuming log-normal errors with standard deviation equal to the root-mean-squared log-scale residual for each data type (see below). Parameters for bootstrap runs were estimated as described for the original run by using the original CV's for each abundance index observation. Thus, our bootstrap runs included process error to the extent that it was reflected in the variance of residuals, and included measurement error to the extent that it was reflected in the original CV's. Two thousand bootstrap iterations were generally used. Asymptotic variance and correlation estimates for parameters were also calculated by inverting a numerical approximation to the Hessian matrix (Bard, 1974; Mittertreiner and Schnute, 1985) because we were interested in comparing the asymptotic and bootstrap approaches.

Parameters with all feasible values positive were estimated as log-transformed values. The log transformation constrains parameters to feasible values on the original scale and improves the statistical characteristics of parameter estimates. Standard errors for log-scale recruitment parameters were transformed to CV's for arithmetic recruitment estimates by using Equation 1.

Results and discussion

Estimates from preliminary runs indicated that availability of age-0 northern anchovy to indices of schooling biomass was close to zero. For final runs, $\rho_{SPOTTER,0}$ and $\rho_{SONAR,0}$ were set to zero and not estimated even though age-0 fish were assumed to be fully recruited to the fishery.

Outliers and residual analysis

Standardized residuals ($D_{t,y}$ in Eqn. 12) for most abundance indexes were serially correlated in preliminary runs. There were two outliers ($D_{EPI,1983}$=3.6 and $D_{SPOTTER,1979}$=3.5) identified by a t-test with Bonferroni p-values (critical value $D_{t,y}$=3.41 for n=77; Weisberg, 1980). Residual plots for the final run with outliers omitted still indicated some serial correlation. All but three biomass estimates for northern anchovy during the 1963 to 1991 fishing seasons increased when the two outliers were omitted. The average increase was 24%.

CV's for abundance indices and goodness of fit

The root-mean-squared residual for each abundance index was calculated to measure how well the SMPAR model fit the data for northern anchovy. Standard deviations were not calculated because degrees of freedom were unknown. Arithmetic CV's implied by the goodness-of-fit statistics were calculated by using Equation 1. For comparison, median CV's for our data (Table 1) were also calculated.

Goodness-of-fit statistics and implied CV's (Table 3) indicate that the CV's for our abundance data underestimated the true log-scale standard errors. The order of abundance indices ranked by median CV's was, however, the same as when they were ranked by goodness of fit. Thus, CV's used in the model reflected the relative precision of different types of abundance data for northern anchovy.

Consistent bias

Percent bias (%BIAS) in biomass and log-scale recruitment estimates for northern anchovy was estimated

Table 3

Goodness-of-fit and CV statistics for northern anchovy, *Engraulis mordax*, abundance indices used in the SMPAR model. Median nominal CV's were calculated from arithmetic CV values in Table 1. Root-mean-squared residuals measure goodness of fit to abundance index. Implied CV's are the arithmetic CV values calculated from the goodness-of-fit measures.

Abundance index	n	Median nominal CV (%)	Root-mean-squared residual	Implied CV (%)
DEP	6	21	0.19	19
EPI	12	31	0.48	51
SPOTTER	27	34	0.49	52
HEP	14	44	0.50	53
SONAR	16	46	0.53	57

$$\%BIAS = \frac{E_{boot} - E_{best}}{E_{best}}, \quad (14)$$

where E_{boot} is the average of estimates from two thousand bootstrap runs and E_{best} is the best estimate from the model fit to the original data. We used the correction factor $\gamma_y = E_{boot} - E_{best}$ to remove consistent bias (Efron, 1982). The corrected estimate of log recruitment in fishing season y, for example, was $\beta_y - \gamma_y$, where β_y was the original biased log-scale recruitment estimate.

Uncorrected log-scale recruitment estimates were biased by amounts ranging from –7% to 7% and arithmetic scale biomass estimates by amounts ranging from –15% to 27% (Fig. 2). Consistent bias was exaggerated when uncorrected recruitments were transformed to arithmetic scale (–40% to 43%, Fig. 3).

Bias from log-transformed recruitment estimates

Arithmetic scale recruitments in each fishing season ($B_{0,y}$) were calculated

$$B_{0,y} = e^{\left(\beta_y - \gamma_y + \frac{VAR(\beta_y)}{2}\right)}, \quad (15)$$

where VAR is a variance estimated by bootstrapping. The term $VAR(\beta_y)/2$ adjusts for bias due to transformation of log-normally distributed random variables (Beauchamp and Olson, 1973). Bias due to log transformation is in addition to consistent bias estimated by $\gamma_y = E_{boot} - E_{best}$. The correction for bias due to log transformation increased northern anchovy recruitment estimates by 1% to 22% (average 9%).

Corrections for bias due to log transformation make arithmetic recruitment estimates for northern anchovy easier to interpret because the amount of bias varies among uncorrected recruitment estimates as a function of their variance. Many stock assessment models (Deriso et al., 1985; Methot, 1990) estimate recruitments as log-scale parameters but corrections for bias in arithmetic-scale recruitment estimates are not made. We recommend that bootstrap or other variance estimates be used to correct arithmetic scale recruitment estimates for bias where appropriate.

Retrospective bias

We evaluated potential for retrospective bias in the SMPAR model by comparing our best biomass estimates to estimates from runs that omitted data for recent years. Bias corrections for retrospective analysis were based on fifty bootstrap iterations. Results indicated a negligible amount of retrospective bias.

Estimates and comparisons

Biomass estimates for northern anchovy age 1 and older from the SMPAR (Table 4) and stock synthesis

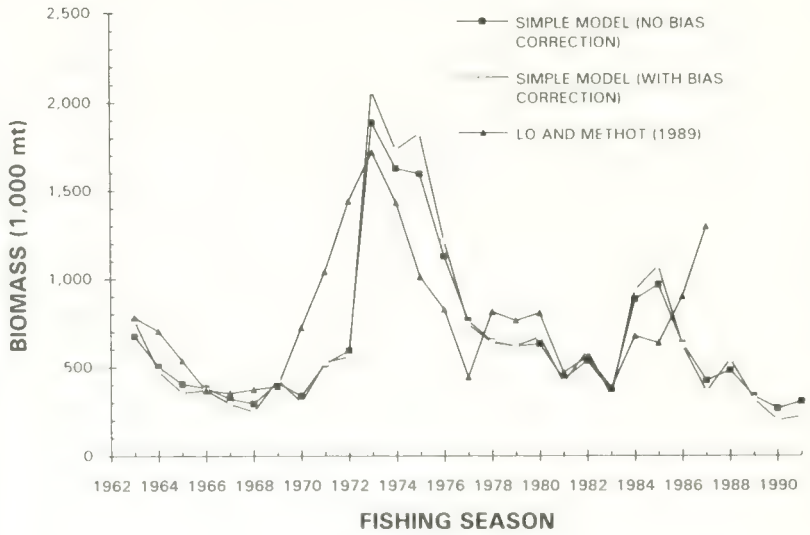

Figure 2

Biomass estimates for northern anchovy, *Engraulis mordax* (age 1+ on 15 February, in thousands of metric tons), during the 1963 to 1991 fishing seasons from the SMPAR model and the stock synthesis model used by Lo and Methot (1989). Estimates from the SMPAR model are shown with and without correction for bias.

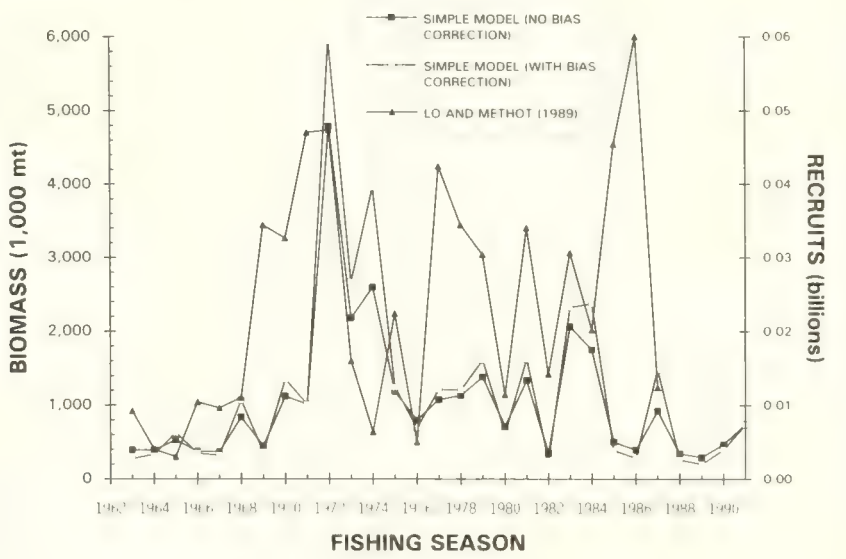

Figure 3

Recruitment estimates for northern anchovy, *Engraulis mordax* (age-0 fish on 1 July, in thousands of metric tons) for the 1963 to 1991 fishing seasons from the SMPAR model (biomass) and the stock synthesis model (number of recruits) used by Lo and Methot (1989). Estimates from the SMPAR model are shown with and without correction for bias.

models were generally similar (Fig. 2) except where retrospective bias in previous estimates was a problem. Results from SMPAR indicate that high northern anchovy biomass in the early 1970's was due to a single large cohort spawned in the 1971 fishing season (age 1 in 1973) rather than to a series of strong recruitments (Figs. 2 and 3). This difference is due to omission of age-composition data and inclusion of SPOTTER data not available to Lo and Methot (1989). Unlike SONAR data, SPOTTER data did not increase significantly until the 1973 fishing season (Fig. 1).

Coefficients of variation for northern anchovy 1+ biomass estimates ranged from 14% to 38% and averaged 26% (Table 4). Precision of the biomass estimate for the most recent fishing season (29%) was better than that from the original stock synthesis model for northern anchovy (CV=40%, Lo et al., 1992). Improvements in data contributed to higher precision, but this result indicates a substantial improvement as a result of using a simpler, more parsimonious model.

Recruitment estimates for northern anchovy from the SMPAR model showed less year-to-year variation than those from the stock synthesis model although both sets of estimates indicate that northern anchovy recruitment was low during the 1963 to 1968 fishing seasons and high in the 1972 fishing season (Fig. 3). CV's for arithmetic-scale recruitment estimates (11% to 69%, average 41%) from the SMPAR model were about 50% larger on average than CV's for biomass estimates (Table 4).

The most important conclusion to be drawn in comparing recruitment estimates from SMPAR with those from the stock synthesis model for northern anchovy is that disparate recruitment estimates (Fig. 3) resulted in similar biomass estimates (Fig. 2). This suggests that abundance index data for northern anchovy contain relatively little information about recruitment variability. The SMPAR model probably underestimates recruitment variability for northern anchovy because it uses only abundance data and includes a recruitment constraint that biases recruitment estimates towards the mean.

Comparison of bootstrap and asymptotic variance estimates

Asymptotic standard errors for parameters obtained by inverting the Hessian matrix were about 19% smaller, on average, than standard deviations obtained by bootstrapping. This result indicates that asymptotic variance estimates for parameters in the SMPAR model were too small.

Sensitivity to weights

We varied weights (λ_i) in the objective function of the SMPAR model to determine how sensitive recent biomass estimates were to different types of data and to the recruitment constraint. Biomass estimates for age 1+ northern anchovy during the 1991 fishing season and average biomass during the 1985 to 1991 fishing seasons were calculated with the weight for each data type set equal to a range of values while other weights were kept at 1.0. Sensitivity analysis for the weight applied to the recruitment constraint (λ_6 in Eqn. 11) is equivalent to a sensitivity analysis on the standard deviation for log-scale recruitments (σ in Eqn. 13). Doubling the weight (λ_6=2.0) is the same as reducing the assumed standard deviation by $1/\sqrt{2}$=0.71. For simplicity, biomass levels in sensitivity analyses were not corrected for bias. SMPAR did not completely converge when the weight for the recruitment constraint was set to 0.0 or 10.0.

Results indicate that current biomass estimates and management advice are affected by weights on EPI data and the recruitment constraint (Table 5). Estimates of anchovy biomass for 1991 were sensitive (changes >10%) to halving (λ_i=0.5) or doubling (λ_i=2.0) weights on EPI data and the recruitment constraint, but estimates of average biomass during 1985 to 1991 were not. Biomass estimates for 1991 were sensitive to removing (λ_i=0.0) EPI data, EPM data, or the recruitment constraint from the model. Average biomass estimates were sensitive to removing EPI, EPM, or SPOTTER data.

Simulation analyses

We used simulation analyses to determine how well SMPAR would estimate biomass under a wide range of recruitment and fishing mortality rates during the 1985 to 1991 fishing seasons. Calculations were the same as those for bootstrapping except that fishing

Table 4

Total, spawning, and recruitment biomass estimates for northern anchovy, *Engraulis mordax*, during the 1963 to 1991 fishing seasons (corrected for bias). Recruitment estimates are for age-zero northern anchovy at the beginning of the fishing season (1 July). Total and spawning biomass estimates are for northern anchovy age 1 and older during the peak spawning period (15 February) of each fishing season.

Fishing season	Total biomass (1,000 t)	CV (%)	Spawning biomass (1,000 t)	CV (%)	Recruitment biomass (1,000 t)	CV (%)	Fishing mortality (yr^{-1})
1963	764	38	734	38	275	43	0.002
1964	477	27	434	31	334	40	0.003
1965	356	24	313	23	627	42	0.023
1966	370	26	311	25	347	42	0.063
1967	293	26	281	26	319	39	0.022
1968	249	25	232	24	1,066	39	0.037
1969	429	26	260	23	364	43	0.111
1970	301	27	232	25	1,348	47	0.074
1971	527	33	195	25	1,008	52	0.045
1972	558	32	547	32	5,941	45	0.020
1973	2,066	34	638	25	2,667	69	0.034
1974	1,733	31	1,243	29	3,955	64	0.042
1975	1,827	30	1,481	27	1,242	54	0.068
1976	1,216	26	1,215	26	693	49	0.120
1977	742	26	741	26	1,211	48	0.132
1978	639	26	530	24	1,204	36	0.172
1979	619	20	607	20	1,611	31	0.121
1980	670	16	630	15	623	35	0.301
1981	415	19	381	17	1,624	22	0.224
1982	589	14	587	14	246	32	0.200
1983	341	14	339	14	2,321	26	0.039
1984	937	20	609	17	2,372	58	0.062
1985	1,072	32	1,057	32	388	35	0.065
1986	620	27	616	27	280	39	0.125
1987	360	24	343	24	1,480	38	0.095
1988	543	27	235	25	261	38	0.120
1989	317	30	309	30	201	37	0.112
1990	199	31	198	31	396	39	0.018
1991	223	29	221	29	739	11	0.005

mortality rates and recruitment levels for 1985 to 1991 were adjusted. For simulations, fishing mortality rates during the 1985 to 1991 fishing seasons were either low (best-fit estimates from actual data, 0.005 to 0.12 yr^{-1}, Table 4) or high (F=1.0 yr^{-1}). Recruitment levels were either low (one third of best-fit estimates in Table 4), equal to best-fit levels, high (three times best-fit levels), or alternating (three times best fit for 1985, one third of best fit for 1986, and so on). There were eight scenarios in total (two fishing mortality patterns combined with four recruitment patterns) and results for each scenario are averages based on fifty simulations. Each scenario used the same series of random numbers to facilitate comparisons.

Results indicate that the SMPAR model is able to track trends in biomass (Fig. 4) under a wide variety of conditions. Uncorrected estimates underestimated year to year variability but this problem would be reduced after bias corrections were applied.

Table 5

Sensitivity of biomass estimates for northern anchovy, *Engraulis mordax*, to weights (λ_i) used in SMPAR. Differences between best-fit results and results with different weights are shown in metric tons and as a percentage of the best-fit estimates. Percentages of values are in parentheses.

Weight (λ_i)	EPI	EPM	HEP	SONAR	SPOTTER	Recruitment constraint
1991 Biomass						
0.0	141	65	–18	2	–4	–55
	(46)	(21)	(–6)	(1)	(–1)	(–18)
0.5	52	–6	–1	7	0	–32
	(17)	(–2)	(0)	(2)	(0)	(–11)
2.0	–50	10	8	–1	2	53
	(–16)	(3)	(3)	(0)	(1)	(17)
10.0	–166	22	22	–31	–17	209
	(–54)	(7)	(7)	(–10)	(–6)	(69)
Mean 1985–91 Biomass						
0.0	–51	–137	–28	12	53	35
	(–10)	(–28)	(–6)	(2)	(11)	(7)
0.5	–11	–14	–1	13	24	0
	(–2)	(–3)	(0)	(3)	(5)	(0)
2.0	7	22	11	–8	–35	10
	(1)	(4)	(2)	(–2)	(–7)	(2)
10.0	–76	53	34	–59	–145	53
	(–16)	(11)	(7)	(–12)	(–30)	(11)

Age composition in the Mexican fishery

Catch curves (Ricker, 1975) for a segment of the Mexican fishery based in Ensenada, Baja California, indicate that age at full recruitment to the Mexican fishery decreased from age 2 to age 0 during 1982 to 1988.[4] Prior to 1983, most year classes reached full recruitment at age 2 but the 1985 and 1986 year classes were fully recruited at about age 1. The trend toward younger recruitment continued with the 1987 and 1988 year classes, which were fully recruited at age 0.

The stock synthesis model interpreted the Mexican age-composition data as evidence for increased recruitment and biomass of northern anchovy. In retrospect, this interpretation seems incorrect because biomass estimates for anchovy declined steadily after the 1985 fishing season (Fig. 2). Declines in biomass were not evident at the time, however, because only one index of relative abundance for northern anchovy (the modified historical egg production index or MHEP, Lo and Methot, 1989) was available, and because recent biomass estimates are relatively uncertain.

Status of the stock

Northern anchovy biomass (Fig. 2) and recruitment (Fig. 3) declined after the 1985 fishing season to about the same levels as during the 1963 to 1971 fishing seasons. Northern anchovy have been too scarce off Baja California, Mexico, to support a fishery since the 1990 season (Table 1). Declines in biomass during recent years were due to low recruitment rather than to high fishing mortality rates because fishing mortality rates were moderate after the 1986 fishing season (<0.14 yr^{-1}) and low (<0.03 yr^{-1}) during the 1990 to 1991 fishing seasons (Table 4). The recent period of low northern anchovy biomass occurred as Pacific sardine, *Sardinops sagax*, biomass levels began to increase in the early 1980's and water temperatures began to warm (Barnes et al., 1992). We

[4] Arenas, P., T. Barnes, and L. D. Jacobson. 1994. Fishery and biological data for northern anchovy taken in Mexican waters, 1978-1989. U.S. Dep. Commer., NOAA, Nat. Mar. Fish. Serv., Southwest Fish. Sci. Cent., P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-94-03, 24 p.

did not attempt, however to identify environmental (Prager and MacCall, 1993) or ecological factors that may have affected northern anchovy abundance in recent fishing seasons.

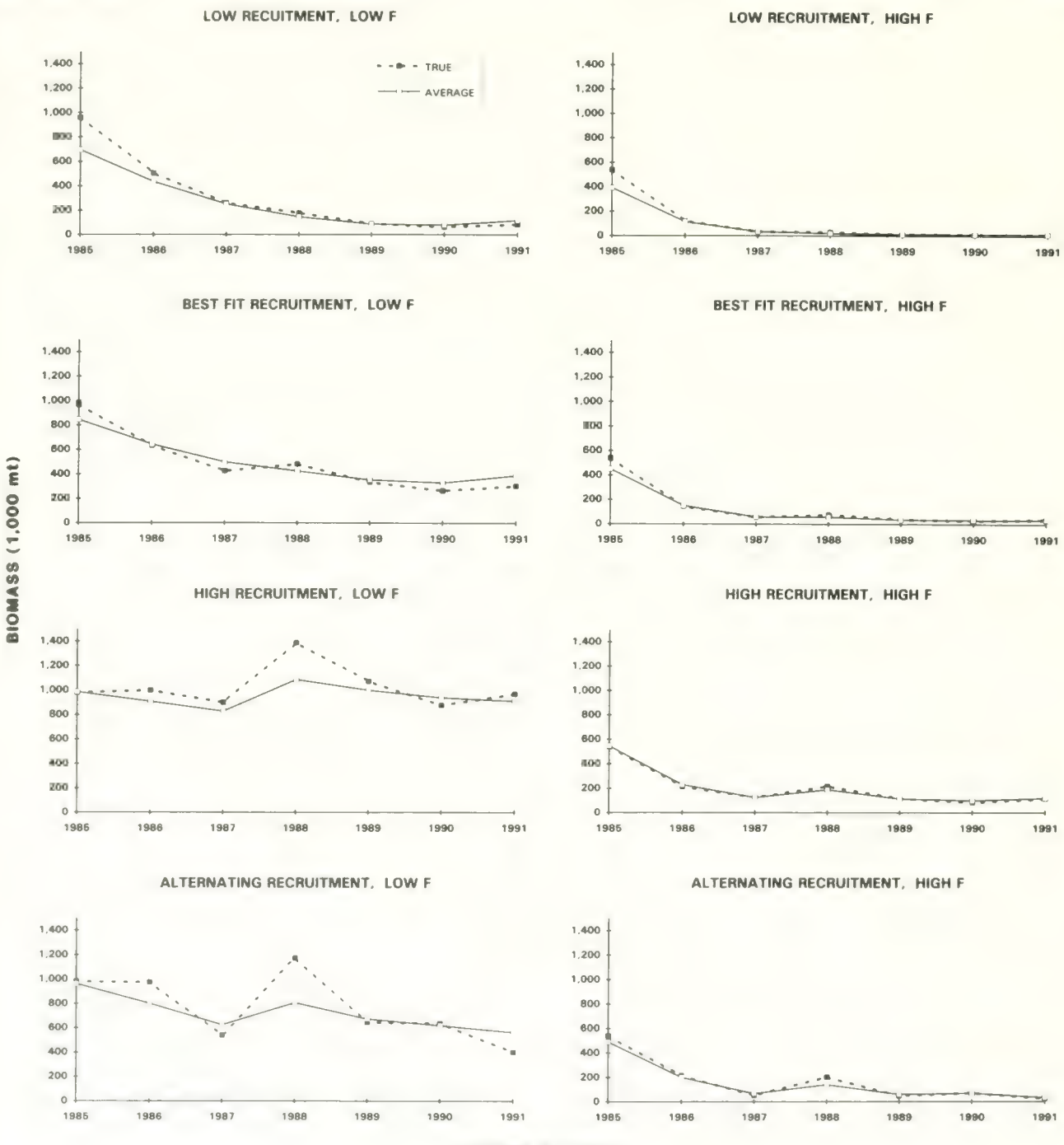

Figure 4

Northern anchovy, *Engraulis mordax*, biomass results (age 1+ on 15 February in thousands of metric tons) for the 1985 to 1991 fishing seasons from simulation analyses. Each panel contains results for one recruitment pattern (low, best fit, high or alternating) and one fishing mortality pattern (low or high). The "TRUE" line in each panel is the true biomass assumed in the simulations. The "AVERAGE" line is the mean of biomass estimates from fifty simulations. Estimates from simulation analyses were not corrected for bias.

Conclusion

Finding the appropriate compromise between realistic (but potentially overparameterized and imprecise) models and parsimonious (but simplistic and potentially biased) models is an important part of a stock assessment research (Ludwig and Walters, 1985, 1989; Hilborn and Walters, 1992). The best choice among models depends on the task, data availability, and complexity of the situation. Our work indicates that models intermediate in complexity between simple surplus production and complex age-structured models can perform well under a wide range of circumstances for estimating the biomass of stocks such as northern anchovy.

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Literature cited

Bard, Y.
1974. Nonlinear parameter estimation. Academic Press, New York, NY, 341 p.

Baxter, J. L.
1967. Summary of biological information on the northern anchovy *Engraulis mordax* Girard. Calif. Coop. Oceanic Fish. Invest. Rep. 11:110–116.

Barnes, J. T., L. D. Jacobson, A. D. MacCall, and P. Wolf.
1992. Recent population trends and abundance estimates for the Pacific sardine (*Sardinops sagax*). Calif. Coop. Oceanic Fish. Invest. Rep. 33:60–75.

Beauchamp, J., and J. Olson.
1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54:1403–1407.

Beddington, J. R., and J. G Cooke.
1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242.

Bence, J. R., A. Gordoa, and J. E. Hightower.
1993. Influence of age-selective surveys on the reliability of stock synthesis assessments. Can. J. Fish. Aquat. Sci. 50:827–840.

Deriso, R. B., T. J. Quinn II, and P. R. Neal.
1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42:815–824.

Efron, B.
1982. The jackknife, the bootstrap and other resampling plans. Society for Industrial and Applied Mathematics, Philadelphia, PA, 92 p.

Gunderson, D. R.
1993. Surveys of fisheries resources. John Wiley and Sons, Inc., New York, NY, 248 p.

Hewitt, R. P.
1988. Historical review of the oceanographic approach to fishery research. Calif. Coop. Oceanic Fish. Invest. Rep. 29:27–41.

Hilborn, R., and C. J. Walters.
1992. Quantitative fisheries stock assessment. Routledge, Chapman, and Hall Inc., New York, NY, 570 p.

Hoenig, J. M.
1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 81:898–903.

Lapointe, M. F., R. M. Peterman, and A. D. MacCall.
1989. Trends in fishing mortality rate along with errors in natural mortality rate can cause spurious time trends in fish stock abundances estimated by virtual population analysis (VPA). Can. J. Fish. Aquat. Sci. 46:2129–2139.

Lasker, R. (ed.)
1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*). U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36, 99 p.

Lo, N. C. H.
1985. Egg production of the central stock of northern anchovy, *Engraulis mordax*, 1951–82. Fish. Bull. 83:137–150.
1986. Modeling life-stage-specific instantaneous mortality rates, an application to northern anchovy, *Engraulis mordax*, eggs and larvae. Fish. Bull. 84:395–407.

Lo, N. C. H., and R. D. Methot.
1989. Spawning biomass of the northern anchovy in 1988. Calif. Coop. Oceanic Fish. Invest. Rep. 30:18–31.

Lo, N. C. H., L. D. Jacobson, and J. L. Squire.
1992. Indices of relative abundance from fish spotter data based on delta-lognormal models. Can. J. Fish. Aquat. Sci. 49:2515–2526.

Ludwig, D., and C. J. Walters.
1985. Are age-structured models appropriate for catch-effort data. Can. J. Fish. Aquat. Sci. 42:1066–1072.
1989. A robust method for parameter estimation from catch and effort data. Can. J. Fish. Aquat. Sci. 46:137–144.

MacCall, A. D., and M. H. Prager.
1988. Historical changes in abundance of six fish species off southern California, based on CalCOFI egg and larva samples. Calif. Coop. Oceanic Fish. Invest. Rep. 29:91–101.

Mais, K. F.
1974. Pelagic fish surveys in the California current. Cal. Dep. Fish and Game, Fish Bull. 162.

Methot, R. D.
1989. Synthetic estimates of historical abundance and mortality for northern anchovy. Am. Fish. Soc. Symp. 6:66–82.
1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data. Int. N. Pac. Fish. Comm. Bull. 50:259–277.

Mittertreiner, A., and J. Schnute.
1985. Simplex: a manual and software package for easy nonlinear parameter estimation and interpretation in fishery research. Can. Tech. Rep. Fish. Aquat. Sci. 1384, 90 p.

Myers, R. A., W. Blanchard, and K. R. Thompson.
1990. Summary of North Atlantic fish recruitment 1942–1987. Can. Tech. Rep. Fish Aquat. Sci. 1743.

Parrish, R. H., D. L. Mallincoate, and K. F. Mais.
1985. Regional variations in the growth and age composition of northern anchovy, *Engraulis mordax*. Fish. Bull. 83:483–496.

Parrish, R. H., D. L. Mallincoate, and R. A. Klingbeil.
1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. Fish. Bull. 84:503–517.

Prager, M. H., and A. D. MacCall.
1993. Detection of contaminant and climate effects on spawning success of three pelagic fish stocks off southern California: northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *Scomber japonicus*. Fish. Bull. 91: 310–327.

Press, W. H., B. P. Flannery, S A. Teukolsky, and W. T. Vetterling.
1990. Numerical recipes. Cambridge Univ. Press, NY.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191.

Sims, S. E.
1982. Algorithms for solving the catch equation forward and backward in time. Can. J. Fish. Aquat. Sci. 39: 197–202.

Sinclair, A., D. Gascon, R. O'Boyle, D. Rivard, and S. Gavaris.
1991. Consistency of some northwest Atlantic groundfish stock assessments. NAFO Sci. Counc. Studies 16:59–77.

Weisberg, S.
1980. Applied linear regression. John Wiley and Sons, NY, 283 p.

Zhang, C. I., and P. J. Sullivan.
1988. Biomass-based cohort analysis that incorporates growth. Trans. Am. Fish. Soc. 117:180–189.

Status of early life history descriptions of marine teleosts

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Abstract.—Use of early life history stages of fish in systematic and ecological studies has increased in recent years. It is now recognized that eggs and larvae present a wide array of characters suitable for systematic analysis that are largely independent of adult characters. Fisheries recruitment studies focus on survival of eggs and larvae as the most important factor influencing variations in population abundance. A requisite to these studies is detailed information on the appearance of fish eggs and larvae in order to identify them in plankton samples. This paper reviews the proportions of fish species for which at least illustrations of eggs and larvae, sufficient to permit their identification in plankton samples, have been published worldwide and by geographic region. Factors which may influence differences in proportion of identifiable eggs and larvae by region are discussed. Factors considered important include species diversity, a history of important commercial fisheries, research emphasis, and interests of individual scientists in various regions. We conclude that although eggs and larvae of most species can now be identified in some regions of the world, there are still gaps in our knowledge that prevent realizing the full potential of ichthyoplankton studies in systematic and fisheries research. Filling these gaps will require continued traditional morphological research as well as application of biochemical genetic and rearing techniques.

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Fish eggs and larvae collected in plankton samples are becoming increasingly important to the study of fisheries, oceanography, and systematics (e.g. Moser et al., 1984; Rothschild, 1986). Accurate identification of early life history stages of fish is a requisite for studies in these fields. Several kinds of publications assist researchers in identifying fish eggs and larvae: 1) some revisions of primarily oceanic groups include descriptions of larvae (e.g. ceratioids [Bertelsen, 1951], bregmacerotids [D'Ancona and Cavinato, 1965], and scopelarchids [Johnson, 1974]); 2) detailed descriptions of the development of a species based on reared or plankton-caught individuals or on a combination of both are common (e.g. Ahlstrom and Ball, 1954; Potthoff et al., 1980; Ditty and Shaw, 1992); and 3) descriptions of several species of a genus or family are also available (e.g. Ahlstrom et al., 1976; Belyanina, 1984; Kendall and Vinter, 1984; Baldwin, 1990).

While these detailed accounts are essential for systematic studies, publications that describe species by geographic region rather than by systematic group are more useful for identification of eggs and larvae from plankton samples. Agassiz (1882), Ehrenbaum (1905, 1909), and D'Ancona et al. (1931–56) are early examples of such publications, and several others have been published recently (e.g. Miller et al., 1979; Auer, 1982; Fahay, 1983; Leis and Rennis, 1983; Wang, 1986; Okiyama, 1988; Leis and Trnski, 1989; Matarese et al., 1989; Olivar and Fortuño, 1991). Besides assisting researchers in identifying fish eggs and larvae in plankton collections, these publications facilitate evaluation of descriptive developmental information available for fishes of a particular region.

In this paper we 1) evaluate the degree to which descriptions of the early life history stages of marine fish are available on the basis of recently published early life history guides, 2) compare our current level of knowledge of fish egg and larva identification by geographic region throughout the world, and 3) discuss potential reasons for regional differences in our level of knowledge.

Methods

We collected information on the status of early life history descriptions primarily from recently published guides on development of fishes in marine waters of seven specific regions of the world (Fig. 1): Northeast Atlantic (Russell, 1976); Northwest Atlantic (Mid-Atlantic Bight) (Fahay, 1983; supplemented by Fahay, 1993); Indo-Pacific (Leis and Rennis, 1983; Leis and Trnski, 1989); Japan (Okiyama, 1988; supplemented by Ozawa, 1986); Antarctica (Kellerman, 1989); Northeast Pacific (Matarese et al., 1989); and Southeast Atlantic (Olivar and Fortuño, 1991). We also used publications that summarized available

descriptive early life history information for two additional geographic regions: the Mediterranean Sea (Aboussouan, 1989) and the west central Atlantic (Richards, 1990). Publications summarizing development of fishes in other major geographic regions (e.g. Southeast Pacific) are not available. We compiled data from the published guides as well as from the more recent, but restricted, publications on the basis of the illustrations of eggs and larvae they contained and then compared our results with those of Richards (1985) who summarized early life history information available at that time based on the work of Moser et al. (1984). We employed six early life history stages (egg, yolk sac, preflexion, flexion, postflexion, and transforming) and considered a particular stage of a species as known if an illustration of that stage had been published. The quality of egg and larval illustrations varies, and we subjectively excluded those that we thought would be inadequate for identifying plankton-collected specimens. Since accurate species lists were not always available in the guides, some subjectivity was involved in determining the number of species present in a region. In cases where the geographic regions covered by early life history guides were more restricted than those considered in regional species lists we used the lists found in the guides. Paxton et al. (1989) was also consulted for the number of species in several regions. Although information was available for eggs and juveniles in some regions, data on larvae were generally used for comparisons because they were more widely available.

To assess the impact of particular scientists on the availability of early life history information on fish for a geographic region, we developed a key author index based on references in Moser et al. (1984). Moser et al. (1984) summarized available early life history information for all fishes, so its bibliography provides an indicator of the contributions of individuals up to about 1982. Key authors were identified as having four or more publications describing the early life history of marine fishes, or as having published a regional compilation of early life history information. The key author index was calculated by dividing the number of publications by key authors by the number of species in a region. Since our purpose here was to indicate the relative amount of research on larval fish taxonomy in various regions, the number of publications was tabulated rather than the number of taxa described. To give a historical perspective, this index was calculated separately for papers published before and after 1950; 1950 was chosen arbitrarily but coincides roughly with increased worldwide harvest of fish following World War II (the world fish catch doubled between 1952 and 1965 [Schaefer and Alverson, 1968]). In the Discussion section we also refer to work done before and after 1900 (as did Ahlstrom and Moser [1981]) to highlight the roots of ichthyoplankton research since the International Council for the Exploration of the Sea was founded in 1898 and since it began field work on fish eggs and larvae in 1901.

To investigate the relationship between commercial fishing activity and the status of early life history information on a regional basis, we compiled regional commerical catch data (Fig. 1) for 10-year intervals between 1938 and 1988 (Food and Agriculture Organization [FAO] 1965, 1974, 1979, 1984, 1991, 1992). The first year that such statistics were available was 1938; so compiling data in 10-year increments should document changes in the regional contribution to the world catch which could be related to changes in early life history information. The reported catches include organisms other than marine fish (e.g. molluscs, crustaceans, and seaweeds), but they are a rather uniform fraction of the total catch, and marine fish represent more than 80% of the total catch. Regional catches in 1938 and 1948 were averaged to represent conditions before 1950, and regional catches in 1958, 1968, 1978, and 1988 were averaged to represent conditions after 1950. The three Antarctic regions (48, 58, 88) used by FAO were combined for our analysis. Catches in the Indian Ocean (51, 57), east central Pacific (77), and west central Pacific (71) were combined to be comparable to the Indo-Pacific region considered by Leis and Rennis (1983) and Leis and Trnski (1989), although the FAO areas included temperate waters not included in Leis and Rennis (1983) and Leis and Trnski (1989). Other FAO regions do not correspond exactly to the regions included in early life history guides (Fig. 1), but at the level of resolution used here such differences are probably insignificant.

To indicate families with the greatest need for additional larval fish taxonomic research, we calculated the ratio of the number of species for which larvae had been described over the number of species present by family for the nine geographic regions for which data were available. It was not possible to calculate this ratio with the data in Aboussouan (1989) or Okiyama (1988). Among those above the median of this ratio, up to 10 per region, families in each region for which this ratio was >0.5, were then ranked on the basis of the number of species they contained.

Results

On a worldwide basis, Richards (1985) concluded that 20,423 fish species were included in the material summarized in Moser et al. (1984). Of these species,

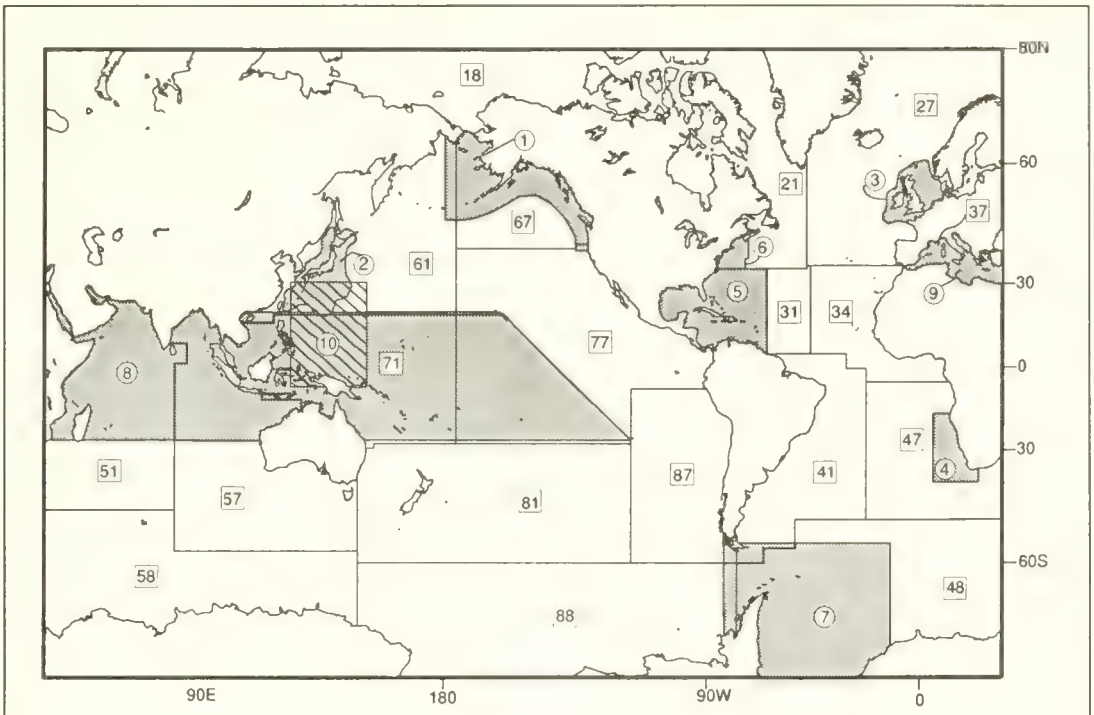

Figure 1

FAO fishing areas (numbers in squares) and areas included in early life history guides (shaded, numbers in circles which are keyed to references in Table 2, except for 10 which refers to Ozawa, 1986). Early life history guides in Indo-Pacific area 8 deal with reef and shore fishes in that area, although oceanic areas are also shaded on the map.

the eggs of 726+ (4%) were known, and larvae of 1,932+ (10%) were known. At a higher taxonomic level, however, larvae of representative species from about two-thirds of the families of marine fishes are known (Ahlstrom and Moser, 1981). Richards (1985) did not subdivide the larval stage as we have (yolk-sac, preflexion, flexion, and postflexion), but most of the illustrations in Moser et al. (1984) are of flexion and postflexion larvae. Although not specifically intended to provide original information for specific identification of fish larvae, Moser et al. (1984) presented many original illustrations.

Regional guides to early life history stages of fishes are now available for nine large areas of the world ocean (Fig. 1). Such guides for both coasts of South America are noticeably lacking, as are guides to most oceanic regions. Some species described in the guides are also found outside the areas specifically covered in these guides; therefore identification of eggs and larvae collected elsewhere is also facilitated by the use of these guides. Some recent guides partially overlap the geographic regions addressed in earlier guides (e.g. Brownell [1979] studied fishes from the Cape of Good Hope, an area that was included in Olivar and Fortuño [1991]; Miller et al. [1979] studied Hawaiian fishes, and their research was included in Leis and Rennis [1983] and Leis and Trnski [1989]; Ozawa [1986] studied oceanic fishes in the areas included in the works of Okiyama [1988], Leis and Rennis [1983], and Leis and Trnski [1989]; and Fritzsche [1978], Hardy [1978, a and b], Johnson [1978], Jones et al. [1978], and Martin and Drewry [1978] studied a portion of the Northwest Atlantic that was included in Fahay [1983]).

We selected the Northeast Pacific as addressed in Matarese et al. (1989) (i.e. the Pacific Ocean and Bering Sea within 200 nautical miles of the coast between lat. 38°N and 66°N and west to long. 180°) for detailed evaluation of the taxonomic composition and available early life history information of the ichthyofauna (Table 1). A total of 627 species of fishes are found in the region, and 592 are thought to spawn in marine waters there (Matarese et al., 1989). These species represent 22 orders and 94 families. The most speciose orders are the Scorpaeniformes (272 species) and Perciformes (140 species). The most speciose families in the Scorpaeniformes are the Cottidae, Cyclopteridae, and Scorpaenidae, and in the Perciformes, the Zoarcidae. While most of the fishes in the Northeast Pacific are oviparous, only about 252 species

(43%) of them are expected to spawn pelagic eggs. Among the Scorpaeniformes, only *Anoplopoma fimbria* is known to have pelagic eggs.

Eggs have been illustrated for only 44 (less than 10%) of the species in the Northeast Pacific, and 8 of these species produce demersal eggs. Eggs are known for 16 of the 31 species of Pleuronectiformes with pelagic eggs (36% of all described eggs). Yolk-sac larvae are known for 90 species of fishes, including 32 species of the viviparous scorpaenid genus *Sebastes* and 18 species of Pleuronectiformes. Preflexion larvae are known for 165 species, flexion larvae for 169 species, postflexion larvae for 217 species, and transforming larvae for 150 species. Some pelagic juveniles are included in the count for transforming larvae, particularly those of the genus *Sebastes*. At least one illustration of an early life history stage is available for 263 species in the Northeast Pacific (44% of the total). To give an indication of the rate of advances in knowledge of the ichthyofauna and its early life history in the Northeast Pacific, since publication of Matarese et al. (1989), one new species has been described (Yabe, 1991), and descriptions of the larvae of seven additional species have become available (Maeda and Amaoka, 1988; Matsui, 1991; Busby and Ambrose, 1993).

The percentage of fishes with descriptive information available on early life history stages varies considerably in various regions of the world (Table 2). Compared with the Northeast Pacific where the eggs of 14% of the species with pelagic eggs are known, only 5% of such species in the western central Atlantic have been identified, whereas the eggs of about 70% of such species are known in the Northeast Atlantic.

Compared with the Northeast Pacific, where the larvae of 44% of the species are known, larvae are known for 34% of the species found in waters around Japan, for 27% of the species in the western central Atlantic, and for only 10% of the species in the Indo-Pacific (Table 2). However, larval illustrations are available for more than half of the species in several geographic regions: Northwest Atlantic, Mediterranean Sea, Southeast Atlantic, Northeast Atlantic, and the Antarctic (Table 2).

Based on early life history guides, the number of species for which early life history information is lacking varies by family and by region (Table 3). Among the families which have larvae described for fewer

Table 1

Taxonomic composition and status of early life history descriptions of northeast Pacific fishes based on Matarese et al. (1989).

Order	Families present	Species present	Number of species illustrated						Species with at least one illustration
				Larval stage					
			Eggs	Yolk-sac	Preflexion	Flexion	Postflexion	Transforming	
Notacanthiformes	1	2	0	0	0	0	0	0	0
Anguilliformes	8	10	0	0	2	2	6	0	6
Clupeiformes	2	5	3	2	3	3	3	2	3
Salmoniformes	7	50	6	2	7	6	12	5	12
Stomiiformes	6	23	2	1	4	10	17	9	18
Aulopiformes	7	10	0	1	4	5	7	5	10
Myctophiformes	2	22	0	2	11	10	15	10	15
Gadiformes	5	19	2	5	7	8	10	7	10
Ophidiiformes	3	10	0	0	3	2	2	0	3
Batrachoidiformes	1	1	0	0	0	0	0	0	0
Lophiiformes	2	7	0	0	0	2	2	2	2
Gobiesociformes	1	2	0	1	2	1	1	1	2
Beloniformes	1	1	1	1	1	1	1	1	1
Atheriniformes	1	2	2	0	2	2	2	0	2
Lampriformes	2	2	1	0	2	0	2	1	2
Beryciformes	5	11	0	0	1	1	2	1	2
Zeiformes	1	1	0	0	0	0	0	0	0
Gasterosteiformes	3	4	0	0	1	1	1	1	1
Scorpaeniformes	6	272	4	46	65	68	79	75	103
Perciformes	26	140	6	11	24	24	36	13	42
Pleuronectiformes	3	32	17	18	25	23	18	16	28
Tetraodontiformes	1	1	0	0	1	0	1	1	1
Totals	94	627	44	90	165	169	217	150	263
Percent of total species			7.0	14.4	26.3	27.0	34.6	23.9	41.9

Table 2

Comparison by geographic region of the number of species with egg and larval illustrations available, key author index, and rank of commercial catches.

Geographic region (FAO areas)	Species present	Number illustrated		Percent known		Source	Key author index		Rank of catches	
		Eggs	Larvae	Eggs	Larvae		<1950	>1950	<1950	>1950
Northeast Pacific (1:67)	592		263	14	44	Matarese et al., 1989	0.000	0.039	—[1]	7
Japan (Northwest Pacific) (2:61)	3500		1181		34	Ozawa, 1986; Okiyama, 1988	0.001	0.042	3	1
Northeast Atlantic (3:27)	131	91	108	70	82	Russell, 1976	0.298	0.008	1	3
Southeast Atlantic (4:47)	239	48	141	20	59	Olivar and Fortuño, 1991	0.017	0.050[2]	8	6
Western Central Atlantic (5:31)	1803	97	486	5	27	Richards, 1990	0.003	0.003	5	9
Northwest Atlantic (6:21)	317	135	222	43	71	Fahay, 1993[3]	0.063	0.146	4	5
Antarctic (7:48,58,88)	158		80		51	Kellerman, 1989	0.000	0.044	12	13
Indo-Pacific (8:51, 57, 71, 77)	3921		394		10	Leis and Rennis, 1983; Leis and Trnski, 1989	0.006	0.007	2	2
Mediterranean Sea (9:37)	569		360		63	Aboussouan, 1989	0.111	0.035	6	10
World	20423	726	1932	4	10	Richards, 1985				

[1] North Pacific not divided into east and west regions.
[2] Olivar and coauthors have published at least nine descriptive papers since 1986 (see Olivar and Fortuño, 1991) that if included here would raise the value to 0.088.
[3] M. P. Fahay (NOAA, Sandy Hook Laboratory, Highlands, NJ 07732, pers. comm. Sept. 1993) indicated that data for the New Jersey area reported here are representative of the Northwest Atlantic.

than half of the species present in several regions are Scorpaenidae, Macrouridae, and Bothidae. Besides these widely distributed families, large proportions of species of families with more restricted ranges are undescribed as larvae, such as the Cottidae in the Northeast Pacific. More species in oceanic families are poorly known as larvae than are indicated in Table 3, because only Ozawa (1986) deals exclusively with that fauna.

Discussion

Factors contributing to variations in the amount of early life history information available among geographic regions include the history of fisheries in the region, the presence of key researchers, and the taxonomic diversity and scientific interest in each region.

History of the fisheries

Generally the geographic regions where larvae of the majority of species are known have had long histories of important fisheries. Studies on fish eggs and larvae were pioneered in the late 1800's by countries that engaged in the fisheries of the Northeast Atlantic (see Hempel, 1979; Ahlstrom and Moser, 1981). Work before 1900 consisted mainly of basic biological studies, sampling eggs and larvae at sea, and rearing eggs and yolk-sac larvae following artificial fertilization for release at sea. Similar studies were initiated concurrently off the east coast of North America. Although during this period the identity of the eggs and larvae of many species was established and knowledge of oceanography of the regions was expanded greatly, these early studies resulted in ill-fated mass releases of young larvae reared in hatcheries on both sides of the North Atlantic (Shelbourne, 1965).

From 1900 to 1950, most early life history studies were conducted on North Atlantic fishes, expanding beyond descriptive work, rearing experiments, and release of young larvae (see Ahlstrom and Moser, 1981). The amount of such research was related to harvest by region. Based on catches in 1938 and 1948,

Table 3

Ranks, by numbers of species, of families with more than half of the species having undescribed larvae, by region.

	Reference and region											
	(Olivar and Fortuno, 1991)	(Leis and Rennis, 1983)	Leis and Trnski, 1989)	Fahay, 1993)	(Russell, 1976)	(Kellerman, 1989)	(Richards, 1990)	(Matarese et al., 1989)	(Ozawa, 1986)			
	Southeast Atlantic	Indo-Pacific Reef	Indo-Pacific Shore	Northwest Atlantic	Northeast Atlantic	Antarctic	Western Central Atlantic	Northeast Pacific	Oceanic West Pacific	Number of times mentioned	Avg rank	Number of times mentioned (10 rank)
Families with >50% of species with undescribed larvae in at least two regions												
Scorpaenidae	5	4		1			9	4		5	4.6	27
Macrouridae	1					3	7	6		4	4.3	23
Bothidae			2				6		2	3	3.3	20
Gobiidae		1					1			2	1.0	18
Cyclopteridae						1		2		2	1.5	17
Myctophidae						2			1	2	1.5	17
Sciaenidae			3				3			2	3.0	14
Blenniidae	4	3								2	3.5	13
Serranidae		6					2			2	4.0	12
Cynoglossidae			6	2						2	4.0	12
Ophidiidae	7						4	9		3	6.7	10
Gonostomatidae								8	3	2	5.5	9
Mugilidae			10		2					2	6.0	8
Engraulidae			4				10			2	7.0	6
Apogonidae	10	5								2	7.5	5
Chaetodontidae		10		10						2	10.0	0

Families with >50% of species with undescribed larvae in only one region, followed by ranks in parentheses

Centrolophidae (2) Labridae (2) Soridae (1) Balistidae (3) Triglidae (1) Labrisomidae (5) Cottidae (1) Melanostomiidae (4)

Sparidae (3) Pomacentridae (7) Carangidae (5) Gerreidae (4) Chaenopsidae (8) Zoarcidae (3)

Gonostomatidae (6) Callionymidae (8) Clupeidae (7) Tetraodontidae (5) Stichaeidae (5)

Moridae (8) Lutjanidae (9) Hemiramphidae (8) Syngnathidae (6) Pholidae (7)

Argentinidae (9) Opisthognathidae (9) Echeneidae (7) Alepocephalidae (10)

Ostraciidae (8)

Diodontidae (9)

the total world catch of all marine species at this time was less than 200 million metric tons (t). Among regions, the Northeast Atlantic ranked first in catches, followed by the western central Pacific, the Northwest Pacific, the Northwest Atlantic, and the western central Atlantic, which together accounted for over 75% of the total catch (Table 2). With the goal of understanding stock fluctuations of Northeast Atlantic fishes, ichthyoplankton studies were conducted largely under the auspices of the International Council for the Exploration of the Sea and this effort is reflected in the state of knowledge for that region. About the same time, similar research was beginning in the Northwest Atlantic. Equally productive research, following work that began in the late 1800's, was being conducted on fishes of the Mediterranean Sea. Early life history studies were also emerging in Japan (where local fisheries have always been vital) with ichthyoplankton surveys beginning in 1938. Work that included descriptions of fish eggs and larvae was also being conducted in India. The western central Pacific and Atlantic contributed significantly to the world catch, and in spite of the immense numbers of species in these regions, progress was made in describing larval fishes there. Larvae of many groups of oceanic fishes were described based largely on collections of the worldwide Dana expeditions and published as Dana Reports. This work resulted partially from interest in the far-reaching early life history of freshwater eels, *Anguilla* spp., which were important to the economy of northern Europe.

Since 1950, early life history knowledge has increased significantly in several regions and is still roughly in proportion to the activity of the fisheries in the regions and countries involved. The total world catch during this period increased to over 800 million t, and the Northwest Pacific replaced the Northeast Atlantic as the most productive region (Table 2). The Southeast Pacific moved from a rank of 11 to 4 among the 14 regions. Earlier, the North Pacific was not divided into east and west portions, but since 1950 the Northeast Pacific was ranked 7, although the catch here was only 15% of that in the Northwest Pacific. Since 1950, Russian scientists have documented early life histories of a wide variety of fishes worldwide as a result of the activity of their distant-water fishing and research fleets. During this time, many fish eggs and larvae from the Northwest Pacific, particularly from waters around Japan, were described. Larvae of most of the fishes of the depauperate Antarctic fauna have been identified as a result of scientific interest and developing international fisheries in the region, although the catches in this region are still insignificant when compared with other regions. Ichthyoplankton studies in the Northeast Pacific initially concentrated on a few commercially important species (e.g. *Sardinops sagax*, *Scomber japonicus*, and *Hippoglossus stenolepis*). The creation of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) in 1947, which targeted research on the Pacific sardine, *Sardinops sagax*, was an important step for egg and larval identification in the California Current region of the Northeast Pacific. Although only 3% of marine species worldwide are expected to spawn in the Northeast Pacific, some species there are very abundant and support large commercial fisheries. Except for the speciose genus *Sebastes*, early life history stages of most commercially important fishes in the region are now well known. Recent catches in the Southeast Pacific ranked fourth among FAO regions worldwide; however, little early life history work has been conducted in this region and larvae of most fishes remain undescribed.

Key researchers

Our use of the bibliography in Moser et al. (1984) to develop a key author index means that some important scientists may not have been included. However, based on the key author index we developed, the contributions of authors who produced multiple descriptions of eggs and larvae of marine fishes have influenced the early life history knowledge of particular geographic regions in terms of the proportion of species whose larvae are known. The key author index for papers produced prior to 1950 is highest (>0.06) in regions where the percent larvae known is also highest (Table 2): Northeast Atlantic (82%), Northwest Atlantic (71%), and Mediterranean (63%). Researchers on eggs and larvae before 1950 in the Northeast Atlantic included Ehrenbaum, Holt, McIntosh, Schmidt, and Petersen (Table 4). In the Northwest Atlantic, early researchers included Agassiz, Breder, Kuntz, and Hildebrand. The Mediterranean has a long history of early life history research where eight key authors including D'Ancona, Padoa, Sanzo, and Sparta were identified for publications before 1950.

Since 1950, the only region with a key author index >0.05 is the Northwest Atlantic, although the index may be inflated because the number of species in the region is probably underestimated. Active researchers in the Northwest Atlantic since 1950 include Eldred, Evseenko, Houde, Leiby, and Smith (Table 4). Other regions where key authors have made notable contributions since 1950 are Japan, the Southeast Atlantic, Northeast Pacific, and the Antarctic. The relatively high taxonomic diversity of

Table 4

Senior authors of four or more publications with original early life history descriptions, or of regional compilations of early life history descriptions based on citations in Moser et al. (1984).

Region	Senior author	Total no. papers	<1950	>1950
Oceanic and >1 region	Belyanina, T. N.	7		7
	Bertelsen, E.	13		13
	Castle, P. H. J.	6		6
	Dekhnik, T. V.	4		4
	Efremenko, V. N.	4		4
	Ege, V.	5	2	3
	Gorbunova, N. N.	7		7
	Pertseva-Ostroumova, T. A.	11		11
	Rass, T. S.	4	1	3
Totals		61	3	58
Mediterranean	Bertolini, F.	2	2	
	D'Ancona, U.	8	7	1
	Fage, L.	2	2	
	Padoa, E.	12	1	11
	Raffaele, F.	1	1	
	Roule, L.	2	2	
	Sanzo, L.	29	28	1
	Sparta, A.	27	20	7
Totals		83	63	20
Number of species		569		
Key author index		0.146	0.111	0.035
Percent larvae known		63		
NE Atlantic	Clark, R. S.	2	2	
	Cunningham, J. T.	3	3	
	Ehrenbaum, E.	5	5	
	Holt, E. W. L.	4	4	
	Lebour, M. V.	3	3	
	McIntosh, W. C.	4	4	
	Petersen, C. G. J.	6	6	
	Russell, F. S.	1		1
	Schmidt, J.	12	12	
Totals		40	39	1
Number of species		131		
Key author index		0.305	0.298	0.008
Percent larvae known		82		
NW Atlantic	Agassiz, A.	2	2	
	Breder, C. M., Jr.	7	6	1
	Dannevig, A.	1	1	
	Eldred, B.	6		6
	Evseenko, S. A.	5		5
	Fahay, M. P.	3		3
	Hildebrand, S. F.	3	3	
	Houde, E. D.	7		7
	Kuntz, A.	4	4	
	Leiby, M. M.	6		6
	Smith, D. G.	9		9
Totals		53	16	37
Number of species		317		
Key author index		0.167	0.050	0.117
Percent larvae known		64		
NE Pacific	Ahlstrom, E. H.	8		8
	Moser, H. G.	8		8
	Richardson, S. L.	7		7
Totals		23	0	23
Number of species		592		
Key author index		0.039	0.000	0.039
Percent larvae known		44		
Japan	Amaoka, K.	10		10
	Dotsu, Y.	11		11
	Fugita, S.	14		14
	Kobayashi, K.	7		7
	Minami, T.	5		5
	Mito, S.	20		20
	Okiyama, M.	18		18
	Shiogaki, M.	13		13
	Suzuki, K.	9		9
	Takita, T.	7		7
	Uchida, K.	4	2	2
	Yusa, T.	9		9
Totals		127	2	125
Number of species		3,500		
Key author index		0.036	0.001	0.036
Percent larvae known		37		
Indo-Pacific	Delsman, H. C.	22	22	
	Fourmanoir, P.	5		5
	Jones, S.	9	2	7
	Leis, J. M.	7		7
	Miller, J. M.	2		2
	Robertson, D. A.	6		6
Totals		51	24	27
Number of species		3,921		
Key author index		0.013	0.006	0.007
Percent larvae known		10		
WC Atlantic	Beebe, W.	5	5	
	Richards, W. J.	5		5
Totals		10	5	5
Number of species		1,803		
Key author index		0.006	0.003	0.003
Percent larvae known		27		
SE Atlantic	Aboussouan, A.	11		11
	Brownell, C. L.	1		1
	Gilchrist, J. D. F.	4	4	
Totals		16	4	12
Number of species		239		
Key author index		0.067	0.017	0.050
Percent larvae known		59		
SW Atlantic	de Ciechomski, J. D	8		8
Antarctic	Yefremenko, V. N.	7		7
Number of species		158		
Key author index		0.044	0.000	0.044
Percent larvae known		51		

fishes in Japanese waters accounts for its low key author index (0.036), but the Japanese probably have been the most prolific scientists working on early life history descriptions since 1950; 125 papers by Japanese key authors were cited in Moser et al. (1984). Even so, Leis (1985) has indicated that the bibliography of Moser et al. (1984) underrepresents the contributions of Japanese scientists. Two early standouts among the Japanese were Uchida and Mito, but recent work by Dotsu, Yusa, Amaoka, Okiyama, Ozawa and Fujita has significantly increased the knowledge of the region. Relatively low taxonomic diversity and an abundance of recent work by Olivar, among others, published since 1986 contributes to a rather high (0.088) key author index for the Southeast Atlantic. In the California Current region the CalCOFI program stimulated early life history descriptions that resulted in many publications by Ahlstrom and Moser (1981) and their coauthors. The Russians, as a result of the activity of their far-reaching fishing efforts since 1950, have contributed to a more complete understanding of early life history of eggs and larvae in several regions through the work of key authors such as Belyanina, Deknik, Gorbunova, and Rass. Also, several Russians, such as Pertseva-Ostroumova as well as non-Russians such as Bertlesen, Castle, and Ege have published papers on early life histories of oceanic groups.

A graph of the cumulative key author index plotted against the percent of the number of species occurring in various regions whose larvae are known, indicates that in all regions where >60% of the larvae are known, the key author index is >0.1 (Fig. 2). Regions with low key author indices (Japan, western central Atlantic, and Indo-Pacific) also have low percentages of known larvae (<40%). However, these regions also have large numbers of species present (Table 2).

Scientific interest and taxonomic diversity

Richards (1985) points out that early life histories of commercially important groups (e.g. herrings, salmons [salmonids], tunas, flatfishes [pleuronectiforms], and cods) have been the subject of a disproportionately greater number of studies and are thus better known than groups that are not the objects of large commercial fisheries. Significant interest in the systematics of particular taxa (e.g. cods in the Northeast Pacific) or the recruitment of particular species (e.g. *Gadus morhua*, *Theragra chalcogramma*, *Clupea harengus*, and *Scomber scombrus*) can lead to increased knowledge of the general early

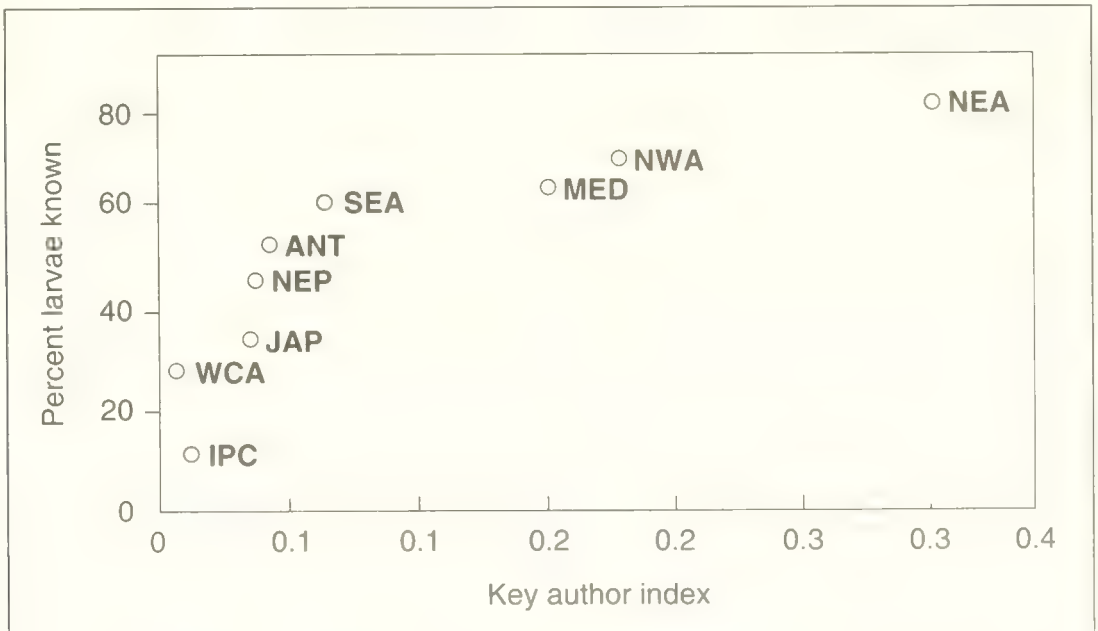

Figure 2

Key author index (see text) plotted against percent of species in geographic regions where larvae are known. ANT=Antarctic; IPC=Indo-Pacific; JAP=Japan; MED=Mediterranean; NEA=Northeast Atlantic; NWA=Northwest Atlantic; NEP=Northeast Pacific; SEA=Southeast Atlantic; WCA=western central Atlantic.

life history of fishes for a region.

The taxonomic diversity of Indo-Pacific coral reefs and Japanese waters is much greater than that found at higher latitudes, resulting in lower proportions of species with identified larvae in these and other low-latitude regions. Speciose perciform families present at lower latitudes contribute to the difficulty of identifying larvae in these regions. In other regions, taxonomic groups that have undergone extensive radiation complicate identification of larvae. For example, about 70 species of *Sebastes* are present in the Northeast Pacific and they cannot be identified routinely in plankton samples (Matarese et al., 1989). The larvae of some closely related taxa in commercially important groups in other regions have proven very difficult to identify (e.g. tunas [scombrids], some herrings [clupeids], and North Atlantic cods [gadids]).

Conclusions

In spite of the relatively large proportions of fishes in some regions for which some early life history stages have been illustrated, identification problems still limit the usefulness of ichthyoplankton studies. For example, in the Northeast Pacific where identification is possible only to family or genus for several groups (e.g. *Sebastes* spp., cottids, agonids, and stichaeids), more descriptive work remains to be done. It is ironic that some groups containing some of the world's most important fisheries (e.g. tunas, cods, and herrings) also pose some of the more difficult problems regarding egg and larval identification. Research involving field studies of fish eggs and larvae in several parts of the world is now concentrating on recruitment dynamics of commercially important species, whose early stages are well described.

Two of the goals of the Ahlstrom Symposium held in 1983 were to accumulate information on fish development by taxa, and thus stimulate additional research on poorly known groups, and to highlight the potential usefulness of developmental information in systematic studies. Since the volume based on the Ahlstrom Symposium was published (Moser et al., 1984), many important original descriptive papers have appeared (e.g. Ditty, 1989; Fahay, 1992), but it does not seem that there has been a significant increase in the number of larvae known. Rather than an increase in original descriptions, the late 1980's saw the publication of several regional guides to fish early life history (see Table 2). While some recent systematic studies have considered larval as well as adult characters (e.g. Cohen, 1989; Baldwin, 1990; Baldwin and Johnson, 1993; Strauss, 1993), there are still unresolved theoretical problems with this approach. Some ichthyologists still do not want to deal with those "unidentifiable pinheads" (Winterbottom, 1986), and rigorous analysis of developmental, in addition to adult, characters can be a daunting task. According to Johnson (1993): "Almost 10 years after its [i.e. Moser et al., 1984] publication the historical separation between studies of early life history stages and 'mainstream' systematic ichthyology appears only slightly diminished. Most comparative osteological and phylogenetic studies of fishes do not incorporate development and thus ignore the potential for additional suites of characters and for testing homology."

A combination of rearing studies and developing series from plankton samples as well as more innovative techniques such as biochemical genetics (Seeb and Kendall, 1991) will be required to fill the gaps in our knowledge on the identification of early developmental stages of marine fishes. Although the value of egg and larval studies are recognized in fisheries science, their usefulness will probably remain limited without the continued efforts of scientists who often describe early life stages as ancillary but enjoyable endeavors.

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Literature cited

Aboussouan, A.
1989. L'identification des larvae de poissons de la mer Méditerranée. Cybium 13:259–262.

Agassiz, A.
1882. On the young stages of some osseous fishes. Proc. Am. Acad. Arts Sci. 16 (Pt. 3):271–303.

Ahlstrom, E. H., and O. P. Ball.
1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. U.S. Fish Wildl. Serv., Fish. Bull. 56:209–245.

Ahlstrom, E. H., and H. G. Moser.
1981. Systematics and development of early life history stages of marine fishes: achievements during the past century, present status and suggestions for the future. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:541–546.

Ahlstrom, E. H., J. L. Butler, and B. Y. Sumida.
1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions and early life histories and observations on five of these from the northwest Atlantic. Bull. Mar. Sci. 26:285–402.

Auer, N. A. (ed.).
1982. Identification of larval fishes of the Great Lakes Basin with emphasis on the Lake Michigan drainage. Great Lakes Fish. Comm. Publ. 82-3, 744 p.

Baldwin, C. C.
1990. Morphology of the American Anthiinae (Teleostei: Serranidae), with comments on relationships within the subfamily. Copeia 1990:913–955.

Baldwin, C. C., and G. D. Johnson.
1993. Phylogeny of the Epinephelinae (Teleostei: Serranidae). Bull. Mar. Sci. 52:240–283.

Belyanina, T. N.
1984. Larvae of hatchetfishes of the genus *Argyropelecus* (Sternoptychidae). J. Ichthyol. 24(2):7–20.

Bertelsen, E.
1951. The ceratioid fishes: ontogeny, taxonomy, distribution, and biology. Dana-Rep. Carlsberg Found. 39, 276 p.

Brownell, C. L.
1979. Stages in the early development of 40 marine fish species with pelagic eggs from the Cape of Good Hope. Ichthyol. Bull. J. L. B. Smith Inst. Ichthyol. 40.

Busby, M. S., and D. A. Ambrose.
1993. Development of larval and early juvenile pygmy poacher, *Xeneretmus trispinosa*, and blacktip poacher, *Xeneretmus latifrons*, (Scorpaeniformes: Agonidae). Fish. Bull. 91:397–413.

Cohen, D. M. (ed.).
1989. Papers on the systematics of gadiform fishes. Nat. Hist. Mus. Los Angeles Co., Sci. Ser. No. 32, 262 p.

D'Ancona, U., and G. Cavinato.
1965. The fishes of the family Bregmacerotidae. Dana-Rep. Carlsberg Found. 64, 92 p.

D'Ancona, U., et al.
1931–1956. Uova, larve, e stadi giovanili de Teleostei. Staz. Zool. Napoli. Fauna e Flora de Golfo di Napoli. Publ. in 4 parts, 1064 p.

Ditty, J. G.
1989. Separating early larvae of sciaenids from the western North Atlantic: a review and comparison of larvae off Louisiana and Atlantic coast of the U.S. Bull. Mar. Sci. 44:1083–1105.

Ditty, J. G., and R. F. Shaw.
1992. Larval development, distribution, and ecology of cobia *Rachycentron canadum* (Family: Rachycentridae) in the northern Gulf of Mexico. Fish. Bull. 90:668–677.

Ehrenbaum, E.
1905. Eier und larven von fischen des Nordischen planktons. Verlag von Lipsius und Tischer, Kiel und Leipzig 1:1–216.
1909. Eier und larven von fischen des Nordischen planktons. Verlag von Lipsius und Tischer, Kiel und Leipzig 2:217–413.

Fahay, M. P.
1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. J. Northwest Atl. Fish. Sci. 4, 423 p.
1992. Development and distribution of cusk eel eggs and larvae in the Middle Atlantic Bight with a description of *Ophidion robinsi* n. sp. (Teleostei: Ophidiidae). Copeia 1992:799–819.
1993. The early life history stages of New Jersey's saltwater fishes: sources of information. Bull. N. J. Acad. Sci. 38:1–16

Food and Agriculture Organization of the United Nations.
1965, 1974, 1979, 1984, 1991, 1992. Yearbook of fisheries statistics, 18, 36, 46, 56, 68, 70. FAO, Rome.

Fritzsche, R. A.
1978. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval, and juvenile stages. Vol. V: Chaetodontidae through Ophidiidae. U. S. Fish. Wildl. Serv., Biol. Prog. FES/OBS-78/12.

Hardy, J. D., Jr.
1978a. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval, and juvenile stages. Vol. II: Anguillidae through Syngnathidae. U. S. Fish. Wildl. Serv., Biol. Prog. FES/OBS-78/12.
1978b. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval, and juvenile stages. Vol. III: Aphredoderidae through Rachycentridae. U. S. Fish. Wildl. Serv., Biol. Prog. FES/OBS-78/12.

Hempel, G.
1979. Early life history of marine fish: the egg stage. Univ. Washington Press, Seattle, 70 p.

Johnson, G. D.
1978. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval, and juvenile stages. Vol. IV: Carangidae through Ephippidae. U.S. Fish. Wildl. Serv., Biol. Prog. FES/OBS-78/12.
1993. Percomorph phylogeny: progress and problems. Bull. Mar. Sci. 52:3–28.

Johnson, R. K.
1974. A revision of the alepisauroid family Scopelarchidae (Pisces: Myctophiformes). Fieldiana Zool. 66.

Jones, P. W., F. D. Martin, and J. D. Hardy Jr.
1978. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval, and juvenile stages. Vol. I: Acipenseridae through Ictaluridae. U.S. Fish. Wildl. Serv., Biol. Prog. FES/OBS-78/12.

Kellermann, A. (ed.).
1989. Identification key and catalogue of larval Antarctic fishes. Biomass Scientific Ser. No. 10., 136 p.

Kendall, A. W., Jr., and B. Vinter.
1984. Development of hexagrammids (Pisces, Scorpaeniformes) in the northeastern Pacific Ocean. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 2, 44 p.

Leis, J. M.
1985. Review of "The bibliography on the identification of the eggs, larvae and juveniles of the marine shorefishes of Japan." Am. Fish. Soc. Early Life Hist. Newsletter 6 (3):11–13.

Leis, J. M., and D. S. Rennis.
1983. The larvae of Indo-Pacific coral reef fishes. New South Wales Univ. Press, Sydney, 269 p.

Leis, J. M., and T. Trnski.
1989. The larvae of Indo-Pacific shorefishes. Univ. Hawaii Press, Honolulu, 371 p.

Maeda, K., and K. Amaoka.
1988. Taxonomic study on larvae and juveniles of agonid fishes in Japan. Mem. Fac. Fish. Hokkaido Univ. 35:47–124.

Martin, F. D., and G. E. Drewry.
1978. Development of fishes of the mid-Atlantic Bight, an atlas of egg, larval, and juvenile stages. Vol. VI: Stromateidae through Ogcocephalidae. U.S. Fish. Wildl. Serv., Biol. Prog. FES/OBS-78/12.

Matarese, A. C., A. W. Kendall Jr., D. M. Blood, and B. M. Vinter.
1989. Laboratory guide to early life history stages of Northeast Pacific fishes. Dep. Commer., NOAA Tech. Rep. NMFS 80, 652 p.

Matsui, T.
1991. Description of young of the mesopelagic platytroctids *Holtbyrnia latifrons* and *Sagamichthys abei* (Pisces, Alepocephaloidea) from the Northeast Pacific Ocean. Fish. Bull. 89:209–219.

Miller, J. M., W. Watson, and J. M. Leis.
1979. An atlas of common nearshore marine fish larvae of the Hawaiian Islands. Sea Grant Misc. Rep. Univ. Hawaii Sea Grant MR-80-02, 179 p.

Moser, H. G., W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall Jr., and S. L. Richardson (eds.).
1984. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Pub. 1.

Okiyama, M. (ed.).
1988. An atlas of the early stage fishes in Japan. Tokai Univ. Press, Tokyo, 1154 p.

Olivar, M. P., and J. M. Fortuño.
1991. Guide to ichthyoplankton of the southeast Atlantic (Benguela Current region). Sci. Mar. 55 (1):1–383.

Ozawa, T.
1986. Studies on the oceanic ichthyoplankton in the western North Pacific. Kyushu Univ. Press, 430 p.

Paxton, J. R., D. F. Hoese, G. R. Hoese, G. R. Allen, and J. E. Hanley.
1989. Zoological catalogue of Australia. Vol. 7: Pisces, Petromyzontidae to Carangidae. Aust. Gov. Pub. Sevr., Canberra, 664 p.

Potthoff, T., W. J. Richards, and S. Ueyanagi.
1980. Development of *Scombrolabrax heterolepis* (Pisces, Scombrolabracidae) and comments on familial relationships. Bull. Mar. Sci. 30:329–357.

Richards, W. J.
1985. Status of the identification of the early life stages of fishes. Bull. Mar. Sci. 37:756–760.
1990. List of the fishes of the western central Atlantic and the status of early life history information. U.S. Dep. Commer., NOAA Tech. Memo NMFS-SEFC-267, 88 p.

Rothschild, B. J.
1986. Dynamics of marine fish populations. Harvard Univ. Press, 277 p.

Russell, F. S.
1976. The eggs and planktonic stages of British marine fishes. Academic Press, London, 524 p.

Schaefer, M. B., and D. L. Alverson.
1968. World fish potentials. *In* Fish (new ser. 4), p. 81–85. Univ. Washington Publ.

Seeb, L. W., and A. W. Kendall Jr.
1991. Allozyme polymorphisms permit the identification of larval and juvenile rockfishes of the genus *Sebastes*. Environ. Biol. Fish. 30:173–190.

Shelbourne, J. E.
1965. Rearing marine fish for commercial purposes. Calif. Coop. Oceanic Fish. Invest. Rep. 10:53–63.

Strauss, R. E.
1993. Relationships among the cottid genera *Artedius*, *Clinocottus*, and *Oligocottus* (Teleostei: Scorpaeniformes). Copeia 1993:518–522.

Wang, J. C.
1986. Fishes of the Sacramento-San Joaquin estuary and adjacent waters, California: a guide to the early life histories. Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary. Tech. Rep. 9 (Available from Ecological Analysts, Inc., 2150 John Glenn Drive, Concord, CA 94520).

Winterbottom, R.
1986. Review of "Ontogeny and systematics of fishes." Bull. Mar. Sci. 39:141–143.

Yabe, M.
1991. *Bolinia euryptera*, a new genus and species of sculpin (Scorpaeniformes: Cottidae) from the Bering Sea. Copeia 1991:329–339.

Catch and effort analysis of the reef fisheries of Jamaica and Belize

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Abstract.—The catch and effort of reef fisheries in seven areas of Belize and in six of south Jamaica were intensively surveyed to provide data for area-based surplus-production models (SPM) to manage these fisheries. Data were normalized to area of productive habitat. SPM's could not be defined for the Belizean or Jamaican data treated separately because the slopes of the relationships between catch per unit of effort and effort were nonsignificant and positive. This appeared to be due 1) to violations of the model's assumptions (catch composition was heterogeneous because fishermen target spawning aggregations and migratory fishes at particular sites) and 2) to possible differences in community composition among areas (the communities were not at equilibrium and productivity possibly differed among sites). Other assumptions had been violated by previous area-based SPM's so that the level of exploitation on the south Jamaican shelf has been seriously underestimated in recent decades. Although a SPM could be defined for the combined Jamaica-Belize data set, we conclude that these models should be used with caution in reef fisheries management because underlying assumptions are likely to be seriously violated. The surveys indicate, however, that levels of catch per unit of effort, catch, and effort in the south Jamaican reef fishery are significantly lower than those of 10 years ago. Depletion of a wide range of fish groups has apparently led to a decline in the equilibrium productivity of the fishery.

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Tropical coral reef fisheries are typically small scale but highly complex, artisanal multispecies fisheries. They are often overexploited (Munro, 1983; Koslow et al., 1988; Russ, 1991) but are rarely managed with conventional fishery methods (see Johannes [1978] on traditional management of reef fisheries). Conventional fishery models are not particularly suitable for complex, multispecies fisheries, and the requisite data, because of the highly decentralized landing and marketing systems typical of these fisheries, is often difficult to obtain. The regions supporting these fisheries often lack the technical and financial resources to manage them, and even if the resources were available, it is arguable whether these small-scale fisheries would justify the expenditure that such an exercise would require. However, although the overall yield of these fisheries is modest, they may provide an important source of employment, protein, and foreign exchange earnings for local economies.

In a pioneering study based on catch and effort data collected during a single survey of landing sites that he grouped by coastal parishes, Munro (1978) developed a preliminary surplus production model (SPM) for Jamaican reef fisheries. His approach was attractive because data inputs and analytic requirements were modest, and the model provided long-term, albeit simple, guidance for optimal fishing levels.

However, the area-based SPM assumes that the fish assemblages, their habitats and productivity, and the fishery do not differ significantly among fishing areas; that the relationship between catch and effort is at equilibrium in each area; and that the fish stocks and effort are contained within the designated fishing areas (Caddy and Garcia, 1982; Nicholson and Hartsuijker, 1982). Nicholson and Hartsuijker (1982), in particular, pointed out the perils of violating the model's assumptions, but area-based SPM's for reef fisheries are being used increasingly to obtain first-order approximations of maximum sustainable yield based upon available catch and effort data (Aiken and Haughton, 1987; Haughton, 1988; Appel-

doorn and Meyers, in press). Area-based SPM's have not been developed further for management of reef fisheries, although more focussed studies have led to interesting results in freshwater systems (Marten, 1979).

Although both are within the Caribbean region, the reef fisheries of Belize and Jamaica contrast markedly. Belizean finfish stocks appear to be lightly to moderately exploited, an assessment not based on quantitative catch and effort data, which have never been systematically collected, but upon the continued availability of prime commercial species (snappers [Lutjanidae] and groupers [Serranidae]) that are the basis of an export-oriented fishery. This assessment is also based on the country's estimated low consumption of seafood; Belize has a sparse population (7.8 persons/km^2 totalling less than 200,000 persons) and has traditionally relied little on seafood. Conch (*Strombus gigas*) and lobster (*Panulirus argus*) are the main focus of Belizean commercial fisheries, followed by snapper and grouper, which are fished primarily for export.

In contrast, seafood is traditionally an important part of the Jamaican diet; the country is densely populated (216 persons/km^2 with a total population of 2,362,000), and its coastal fisheries have been heavily exploited for at least the past several decades (Aiken and Haughton, 1987). Since 1970, catch rates in the reef fisheries have markedly declined (Aiken and Haughton, 1987; Haughton, 1988), and the catch composition has shifted to commercially less valuable species (Koslow et al., 1988). Snappers, groupers, and large parrotfishes (Scaridae) that were abundant off Jamaica in the last century (Gosse, 1851) have virtually disappeared from most reef areas.

Our objective was to develop a SPM to manage the reef fisheries of Jamaica and Belize. To improve upon previous area-based SPM's, we carried out focussed surveys of catch and effort to better quantify the model in relation to some of its underlying assumptions. In particular, we assessed the productive area underlying each fishery by estimating the proportion of productive reef habitat in different parts of the shelf and by localizing the fishing grounds used, and we quantified annual fishing effort. By surveying reef fisheries in these two countries, we hoped to relate catch and effort over a range of exploitation rates and develop a broadly applicable SPM.

Methods

Field study

A two-phase survey was carried out in Belize and along the south coast of Jamaica (Fig. 1, A and B). First, a stratified systematic survey was carried out to determine the numbers of fishermen by region, the types of vessels and gears in use, and the grounds fished, and to obtain general information on effort, catch, and seasonality in catch composition and abundance. Validated lists of fishing vessels in the two countries were obtained from the licensing registers of fisheries departments and from surveys of landing sites (20 active fishing beaches on the south coast of Jamaica and 10 cooperatives and markets in Belize). The lists were stratified by area and a sample from each area was systematically selected. A questionnaire was administered to the selected fishermen in Belize, but owing to difficulties in locating selected fishermen in Jamaica, a number of fishermen were chosen from those available on the fishing beaches.

Based on this survey, the fishing grounds were subdivided into seven areas in Belize and six in Jamaica. However, spawning aggregations fished in several of the areas in Belize accounted for a significant proportion of the fish landings and seemed likely to draw fish from nearby areas. In calculating the SPM, data from areas 4 and 5 (east and west Ambergris Cay) were pooled, as were data from areas 2, 3, and 7 (Fig. 1B).

In the second phase of the survey, six landing sites in Jamaica and five in Belize were visited to collect data on effort and landings over an annual cycle. Thus one site that was deemed representative was selected from each area, except in Belize City (Gallows Pt.) area, where two cooperatives were visited. Sites were visited every two weeks in Belize between July 1990 and August 1991 (except Placencia, which was sampled from March through August 1991) and in Jamaica from February through April and August through November 1991. Sites were monitored for the entire period during which fish were landed. As each vessel landed its catch, overall weights were recorded by family, and fishermen were interviewed to ascertain the gears used, the effort by gear-type, and the areas fished. In Jamaica, there were too many vessels at some sites to monitor all landings. In these instances, total effort and landings statistics for the site were estimated by the proportion of vessels actually surveyed: $X_T = X_t/F$, where X_T is the total landings or effort for a site on a particular day, X_t is the landings or effort recorded, and F is the proportion of vessels surveyed.

The effective area of the fishing grounds in each area was estimated. The total area of the shelf was estimated from charts both with a planimeter and by weight, whereby the shelf area was traced from a chart, cut out, weighed, and the weight related to that of a unit area (e.g. 10 km^2). The extent of the actual fishing grounds was determined from interviews conducted during the surveys. In Belize, the

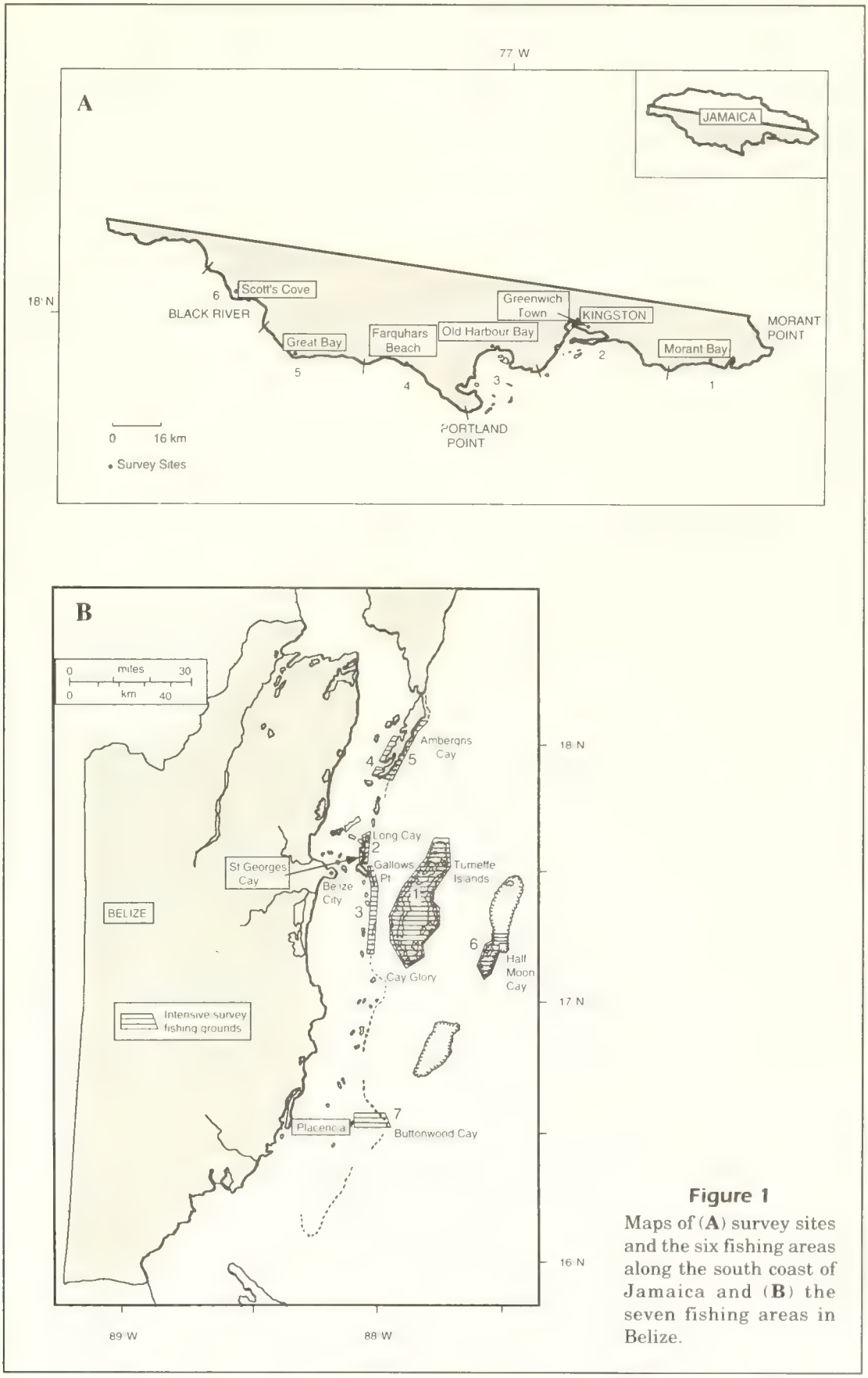


Figure 1

Maps of (**A**) survey sites and the six fishing areas along the south coast of Jamaica and (**B**) the seven fishing areas in Belize.

fishermen noted their fishing grounds on a chart in relation to the cays, and the fishing grounds were assumed to extend to the reef crest. The areas of these grounds were then measured with a planimeter.

In Jamaica, four line transects orthogonal to the shoreline from nearshore to the shelf edge were carried out in each of three areas: Old Harbour Bay, Farquhars Beach, and Great Bay (Fig. 1A). Transects within each area were approximately 2 nmi (=3.7 km) apart. The mean depth of the south Jamaican shelf is 20 m (Woodley and Robinson, 1977), and the dropoff is at about 50 m (Nicholson and Hartsuijker, 1982); observations of bottom type were made with a glass-bottomed viewing box deployed over the side of a small vessel. Observations were carried out at 4-km intervals of the dominant substrate material (i.e. sand, grass, coral, or mud). The proportion of shelf represented by each substrate type was estimated from the proportion of stations at which the particular substrate type was dominant. The results of these surveys were compared with historical surveys of the Jamaican shelf (Nicholson and Hartsuijker, 1982).

Data analysis

Catch and effort data were summed by area, gear type, and species group. Totals were standardized by proportions of the fishing year and of the population of fishermen surveyed. Fishing effort in a SPM must be expressed in a common unit. Hook-and-line effort (hook h/km^2) was selected as the common unit of effort because our surveys indicated that it was the dominant fishing gear in Belize (in terms of incidence of use and yield obtained) and the most widely used gear overall. Fishing effort from other gear types (i.e. bottom gill net, trap, weir, and spearing) was standardized to hook-and-line gear by using the weighted mean of the ratio of catch rates from the particular gear to the hook-and-line catch rate within each area. Effort was then summed within each area.

Catch and effort for each area were standardized per square kilometer of fishing ground. Log-transformation of the catch-per-unit-of-effort (CPUE) data (the Fox [1970] variant of the SPM) did not improve the fit, so it is not presented. However, the relationship between CPUE and effort (f) was highly nonlinear; therefore, the relationship is presented both without transformation and with effort data log-transformed, which linearized the relationship between CPUE and f.

Results

Catch and effort

Annual catch was estimated to be more than four-fold higher off the south coast of Jamaica (998 tonnes) than off the coast of Belize (240 tonnes) (Table 1). When landings were normalized to the area of productive fishing ground (Tables 1 and 2) (i.e. the portion of shelf estimated to be coral and sea grass), yield per unit of area from Jamaican waters (552 kg/km^2) was 39% higher than off Belize (340 kg/km^2). However, this difference was not statistically significant in a comparison of mean yield from the different fishing areas in the two countries (Kruskal-Wallis [KW] one-way ANOVA: χ^2=0.33, n=13, P>0.2).

Table 1

Catch (Y) and fishing effort (f) data summary for sites in Belize and Jamaica. See Figure 1 for areas.

Country	Site	Area (A) (km^2)	Total Y (t)	Prime Y (t)	Total f ('000 hook h)	Y/A (kg/km^2)	f/A (hook h/km^2)
Belize	1	312	30	26	22	97	71
	2	32	7	7	3	208	86
	3	47	31	24	34	655	720
	4	10	16	14	15	1,688	1,505
	5	33	8	4	9	250	275
	6	231	18	17	15	79	65
	7	44	130	126	52	2,929	1,172
Jamaica	1	46	55	8	286	1,197	6,209
	2	252	344	159	2,038	1,364	8,089
	3	607	265	51	1,303	437	2,147
	4	652	266	18	1,448	409	2,222
	5	115	37	4	265	319	2,307
	6	135	31	6	257	223	1,901
Totals	Belize	709	240	218	150	340	210
	Jamaica	1,807	998	246	5,597	552	3,098

Table 2

The shelf area of the south Jamaican shelf and the proportions represented by coral, seagrass, sand, and mud benthic habitat types. The regions are shown in Figure 1A.

Region	1	2	3	4	5	6	Total
Total shelf area (km^2)	127	331	797	1,390	316	372	3,333
Proportion of coral	0.32	0.48	0.48	0.22	0.32	0.32	0.33
Proportion of seagrass	0.05	0.28	0.28	0.25	0.05	0.05	0.21
Proportion of sand	0.32	0.15	0.15	0.34	0.32	0.32	0.27
Proportion of mud	0.32	0.09	0.09	0.19	0.32	0.32	0.19

The fishing effort and catch rates of the two countries differed considerably. The mean fishing effort per unit area on the Jamaican grounds was fifteenfold higher than off Belize: 3,098 hook h/km^2·yr (equivalent to 527 trap hauls/km^2) in Jamaica and 210 hook h/km^2·yr in Belize (KW: χ^2=9.00, P<0.005). However, catch rates were ninefold higher in Belize: 1.61 kg/hook h compared with 0.18 kg/hook h (equivalent to 1.06 kg/trap haul) in Jamaica (KW: χ^2=9.00, P<0.005).

Catch composition

The composition of the fishery also was substantially different in the two countries (Fig. 2). Prime commercial fishes from the Lutjanidae (snappers) and Serranidae (groupers) dominated the Belizean fishery, representing 74% and 11% of the catch, respectively. In contrast, lutjanids represented 23% of the Jamaican catch and serranids only 2%. Of the landings in Jamaica, 62% were of low-value species, fishes in the families Scaridae, Sparidae, Labridae, Mullidae, Holocentridae, and Acanthuridae. Another 14% were haemulids, which composed only 2% of the catch in Belize. When the data were aggregated by area, the differences in catch composition between the countries were all significantly different (Table 3), as were the differences in actual catch for all groups except lutjanids. The catch of serranids was significantly higher in Belize and that of haemulids and 'other' fish was higher in Jamaica. When the data were examined on the basis of individual landings, the number of degrees of freedom was greatly increased. Differences were highly significant for all groups: landings of serranids and lutjanids were again higher in Belize; landings of haemulids and 'other' fishes were higher in Jamaica (Table 3).

Within each country, species composition also varied significantly among fishing grounds (Fig. 2). Landings of the main species groups were approximately log-normally distributed among regions within each country, especially in Belize, where landings per unit of area generally varied among fishing grounds by two to three orders of magnitude. In Jamaica the differences were generally closer to two orders of magnitude. Thus in Belize, landings per unit of area of lutjanids were highest in areas 4 (west Ambergris Cay) and 7 (Placencia); of serranids in areas 3 and 4 (Gallows Point and west Ambergris Cay); and of haemulids in areas 3 and 5 (Gallows Pt. and east Ambergris Cay). Several of these areas were sites of major spawning aggregations (S. Auil, unpubl. data). The outer atolls, Halfmoon Cay and Turneffe (areas 1 and 6), did not appear to be intensively fished for finfish. In Jamaica, lutjanid and haemulid landings were higher in areas 1 and 2; serranid landings were higher in areas 2 and 3. The catches of low-valued fish were more evenly distributed.

Surplus production models

Because of the heterogeneity of the fishery, we examined catch-effort relationships for species groups, both individually and combined. The slopes of the relationships of CPUE with effort (f) were nonsignificant but were positive in sign for the Jamaican and Belizean reef fisheries considered separately (Table 4). When the data for the two countries were combined, the relationship between CPUE and f was negative (Table 4, Fig. 3A). A linear relationship, obtained after log-transforming the data on f, was due largely to the substantial difference in f and CPUE between the two countries (Fig. 3B). Based upon these relationships, MSY for the total reef fisheries was estimated to be 1,046 kg/km^2 of productive

Table 3

Results of Kruskal-Wallis one-way ANOVA to test for differences in catch composition between Jamaica and Belize for the data shown in Figure 2. (**A**) test for differences in proportion of catch by fish groups aggregated by area (n=13); (**B**): test for differences in landings of fish groups aggregated by area (n=13); (**C**): test for differences in landings by individual landing (n=503). The statistic shown is the χ^2 value. *P≤ 0.05; **P≤ 0.01; ***P≤ 0.001. NS = not significant.

	Lutjanidae	Serranidae	Haemulidae	Other
A	7.37**	6.61*	4.00*	7.37**
B	2.47 NS	5.22*	4.00*	4.00*
C	19.42***	38.2***	52.6***	12.2***

habitat (sea grass+coral), with an annual fishing effort (f_{msy}) to obtain MSY of 3,497 hook h/km^2 (Fig. 4A). Current fishing effort in Jamaica and Belize (Table 2) is 89% and 6% of f_{opt}, respectively. MSY for the piscivorous fishes (e.g. Serranidae, Lutjanidae, and Sphyraenidae) was estimated to be 638 kg/km^2 of productive habitat, which can be caught at f_{msy} = 2,200 hook h/km^2 (Table 4, Fig. 4B). To maximize catch of piscivorous fishes, present fishing effort in Jamaica and Belize is 141% and 10% of f_{msy}, respectively.

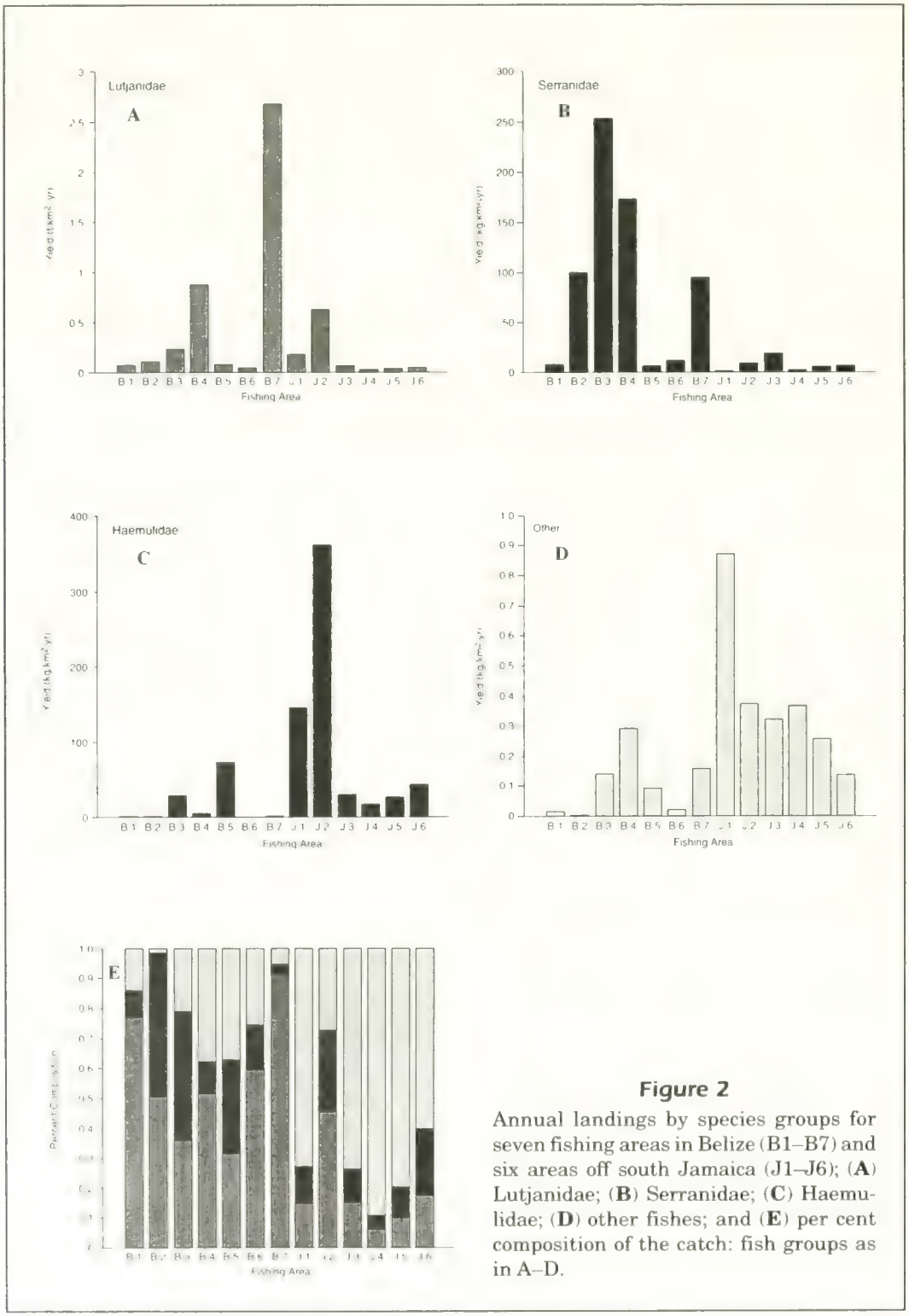


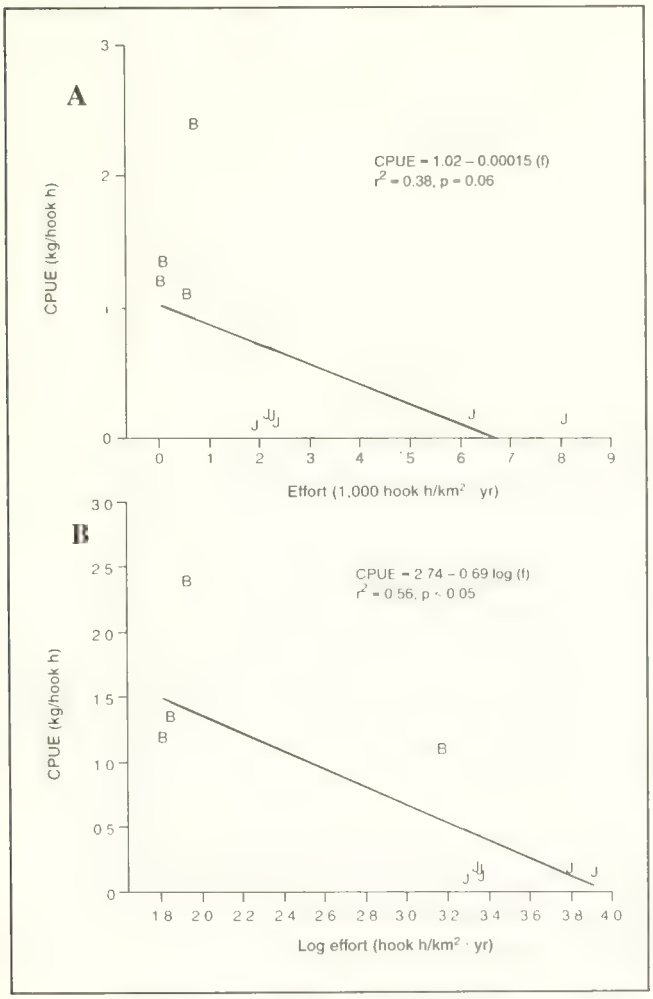
Figure 2

Annual landings by species groups for seven fishing areas in Belize (B1–B7) and six areas off south Jamaica (J1–J6); (**A**) Lutjanidae; (**B**) Serranidae; (**C**) Haemulidae; (**D**) other fishes; and (**E**) per cent composition of the catch: fish groups as in A–D.

Table 4

Surplus production model based upon Jamaica and Belize fishery data. Results of regressions between catch per unit of effort for all reef fish (Total CPUE) and prime commercial species (Prime CPUE) with fishing effort (f). Maximum sustainable yield (MSY) cannot be estimated for regression models for Belize and Jamaica data separately because the slopes are positive. Regression models for prime commercial species for Belize and Jamaica separately also had nonsignificant positive slopes and are not shown. R^2=% variance explained; P=probability level; f_{msy}=f at MSY.

Model	Area	R^2 (%)	P	Slope	Intercept	MSY (kg/km^2)	f_{msy} (hook h/km^2)
Total CPUE/f	Belize	20	0.56	0.00048	1.21	—	—
Total CPUE/f	Jamaica	3	0.79	$2.0 \cdot 10^{-6}$	0.17	—	—
Total CPUE/f	Jamaica and Belize	38	0.06	$-1.5 \cdot 10^{-4}$	1.02	1,720	3,357
Prime CPUE/f	Jamaica and Belize	39	0.07	$-1.4 \cdot 10^{-4}$	0.85	1,253	2,942
Total CPUE/Log(f)	Jamaica and Belize	56	0.02	−0.69	2.74	1,046	3,497
Prime CPUE/Log(f)	Jamaica and Belize	54	0.02	−0.67	2.52	638	2,200



Discussion

Differences in catch composition between the two countries largely arose from the greater abundance of lutjanids and serranids in Belize. However, there may be several contributing factors. The Belizean fishery largely targets fishes for export, and only a narrow range of species, primarily lutjanids and serranids, are marketable overseas. In Jamaica, there is a large domestic market, in which a wide range of fishes may be sold. Furthermore, the predominant fishing gear in Belize is hook-and-line, which selectively catches piscivorous fishes, whereas the predominant gear in Jamaica is the Antillean fish trap, which catches a greater diversity of fishes. Less desirable species may be discarded in Belize, whereas in Jamaica, virtually all species are marketed locally. However, lutjanids and serranids are also considered prime commercial species in Jamaica, and local hook-and-line fisheries target lutjanids in particular. Thus if these groups were more abundant, they would represent a greater proportion of the catch. Historical records show that they were formerly caught in quantity by fish traps off south Jamaica (Gosse, 1851).

Figure 3

The fit of total catch of reef fish per unit of effort (CPUE) in relation to fishing effort (f) for fishing grounds in Belize (B) and Jamaica (J). (**A**) Fishing effort on an arithmetic scale; (**B**) fishing effort on a logarithmic scale.

Results of the SPM suggest that the Belize fishery is capable of further expansion in most areas but that Jamaican fishing areas are overfished. Current levels of effort in Belize seem to be only 10% of the levels that would maximize landings of prime commercial species. Landings are presently at about half of MSY for this group (Table 5). This is not surprising because many Belizean fishermen report that this fishery is virtually incidental to their lobster fishery. In Jamaica, on the other hand, present fishing effort is 41% above the level that would maximize the catch of prime commercial species, but effort is below the level predicted to maximize total fish landings. However, the low present catch of prime commercial species in Jamaica relative to their apparent potential (21% of MSY) is clearly due to the effects of overfishing rather than to under-exploitation.

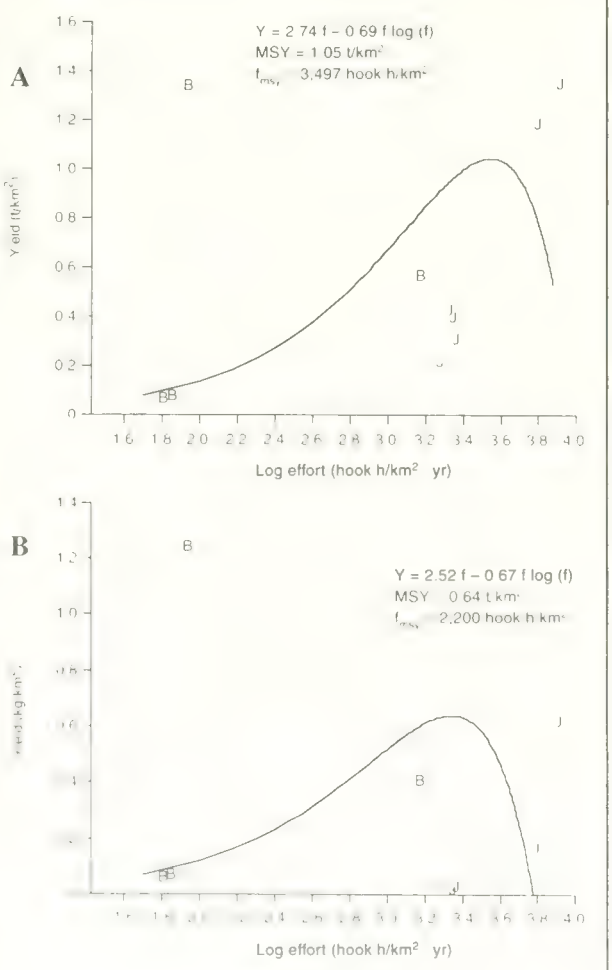


Figure 4

The relationship of fish yield (Y) to fishing effort (f) for reef fishing grounds in Belize (B) and Jamaica (J). (**A**) The relationship for total yield of reef fish; (**B**) the relationship for prime commercial species.

The model's predictions must be regarded with caution, however, because of the poor fit of the SPM data. The relationships of CPUE and f within countries were nonsignificant but positive (Table 4). When the relationship between CPUE and f is non-negative, MSY cannot be estimated: the relationship of yield (Y) with effort (f) continues to increase rather than attain a maximum. Although a negative slope might be obtained if particular data points were removed, there was no objective basis for doing this. Thus, when data from Belize and Jamaica were pooled, the negative slope of the regression between CPUE and f was predominantly based upon the relationship between countries. This decreases the effective number of degrees of freedom and diminishes confidence in the estimate of MSY. The estimate may, therefore, serve to establish initial levels of MSY, but if time series of catch and effort are developed in the two countries, the present relationship is likely to be modified and should be reevaluated for each fishery and country as data allow.

The lack of significant relationships between CPUE and f within the Jamaican and Belizean reef fisheries may arise from several factors: heterogeneity of the fishery among areas; mixing of fish stocks between fishing areas or migration of fish into or out of these areas; and disequilibrium of the fisheries in the different areas. All of these factors appear to be present, although their relative importance is unclear.

Heterogeneity is apparent from the differences in composition of the catches within countries as well as between them. Heterogeneity was noted when landings were classified at familial or broader taxonomic groupings and likely is greater at the species level.

Movements of fishes among areas were noted particularly in the Belizean fishery, which is based upon a mix of targeted fishing on spawning aggregations and fishing on the nonspawning, more dispersed phase of the populations. CPUE may be expected to vary between these two phases of the fishery, thereby confounding the use of a spatially based surplus production model. Separation of these two phases of the fishery is difficult. CPUE is a function of both the degree of aggregation (or behavior) of the fish and of their abundance, which is presumably affected by total f. Therefore, data cannot be used from only one phase of the fishery. Furthermore, the catchability of a particular gear—and hence its impact per unit of f upon fishing mortality—presumably varies between the different phases of a fishery. It may therefore be necessary to standardize each gear type between different phases of the fishery, as well as to standardize among gears.

Jamaican, and perhaps Belizean, reef fisheries may be in a state of flux, which violates the model's as-

Table 5

Comparison of present levels of total and prime commercial fish yields (Y) and fishing effort (f) with maximum sustainable yield (MSY) (in tonnes) and f at MSY (f_{msy}) (in thousands of hook h) predicted by the surplus production model.

	Present fishery			Model			
	Total Y (t)	Prime Y (t)	f ('000 hook h)	Total MSY (t)	Prime MSY (t)	Total f_{msy} ('000 hook h)	Prime f_{msy} ('000 hook h)
Belize	241	216	149	742	452	2,480	1,560
Jamaica	998	247	5,598	1,890	1,153	6,317	3,974

sumption of equilibrium. In Jamaica, one index of fishing effort, the number of fishing canoes, appears to have declined by 55% over the past decade. In a 1981 survey, 2,137 fishing canoes were recorded along the south coast (Haughton, 1988) but only 963 in the present study. (Because the fishery could be easily censused, the number of canoes on fishing beaches was the primary measure of fishing effort in most previous studies of Jamaican reef fisheries [Munro, 1978, 1983; Haughton, 1988]). Landings of fish from the south Jamaican shelf declined 82% during this decade from 5,475 metric tons (t) in 1981 (Haughton, 1988) to 998 t in 1991. The decline in landings and effort resulted in a 60% decline in CPUE from 2.56 to 1.04 t/canoe·yr. The decline in fishing effort may be a consequence of falling catch rates. The datum for CPUE in relation to f for 1991 does not fall along the line defined by the 1968–1981 data for the Jamaican fishery (Fig. 5), possibly because the fishery is not at equilibrium, that is, it has not recovered in response to recently reduced effort.

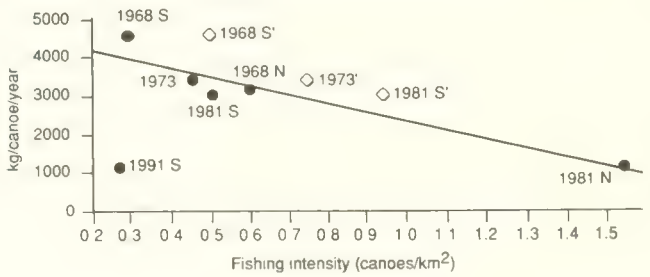


Figure 5

The relationship of catch per unit of effort for the Jamaican reef fisheries based upon data from 1968 to 1981 (from Haughton, 1988) and from the present study. Data are shown for reef fisheries off the north (N) and south (S) coasts of Jamaica. (') indicates data from the southern shelf that have been corrected for the proportion of reef and sea grass habitat. The regression line is based upon the original, uncorrected data from 1968 to 1981.

It may be expected that estimates of sustainable yield and effort obtained from the present survey would be significantly lower than previous estimates owing to reduced levels of CPUE, catch, and effort. Munro (1978) estimated that MSY for the Jamaican reef fisheries was 4.1 t/km^2 and that f_{msy} was 3.2 canoes/km^2 shelf area. These estimates were based primarily on data from the north coast, where the shelf is narrow and much of the substrate is coral, therefore they are probably comparable to our estimates based upon the coral and sea-grass fraction of the south Jamaican shelf. Munro's spatially based SPM used data from a 1968 fishery survey. Haughton (1988) developed an SPM for the Jamaica reef fishery based upon three fishery surveys of the north and south Jamaican shelves conducted between 1968 and 1981. Differences in the productivity per unit area of the north and south Jamaican shelf were not considered. Haughton estimated MSY for the south Jamaican fishery to be 2.2 t/km^2 of shelf with an f_{msy} of ~1 mechanized canoe/km^2. (The units of effort of the Munro and Haughton models are not entirely comparable because most canoes became mechanized after Munro's survey; Haughton standardized his effort data to the mechanized canoe.) If the data for the southern shelf in Haughton's model are normalized per unit of area of productive habitat (~50% of the total shelf area), so that data from the north and south coast are comparable, the revised estimates of MSY and f_{opt} are 3.1 m/km^2 and 1.5 canoes/km^2 of productive habitat. However, there is no longer a significant relationship between CPUE and f (Fig. 5). Our estimate of MSY for the combined Jamaican and Belizean reef fisheries is 1.0 t/km^2 (Table 4). Based upon present effort in Jamaica being 89% of f_{opt} (f=3,099 hook h/km^2 [Table 2]; f_{msy}=3,497 hook h/km^2 [Table 4]), f_{msy} may be estimated to be approximately 0.6 canoes/km^2 of productive habitat; the present density of canoes is 963 canoes over a productive shelf

area of 1,807 km^2 or 0.5 canoes/km^2). Thus, present estimates of MSY and f_{msy} are on the order of 20–30% of earlier estimates.

Declining levels of CPUE, catch, and effort in the south Jamaican fishery and lower estimates of sustainable yield and effort all indicate that the productivity of Jamaican reef fishes significantly declined because of overfishing. The species composition of the trap fishery in the 1800's appears to have been broadly similar to that off Belize today (Gosse, 1851). By 1968–71, when the first research surveys on the south Jamaican shelf were carried out, the catch was already dominated by relatively low-value fish: the Haemulidae, Scaridae, and Acanthuridae (Munro, 1983). By 1986, when these surveys were repeated, overall CPUE had declined 33%. Several families across a wide trophic range that represented the bulk of the catch in 1968–71 had declined by more than 50% (haemulids, small serranids, and acanthurids) or virtually disappeared (large serranids and large scarids) (Koslow et al., 1988). The Holocentridae and Pomacentridae were the only families that increased significantly. Thus large segments of the demersal fish community may be depleted on reefs overfished by traps. This is in contrast to reefs exploited by more selective gear, such as spears that target large piscivores, where a range of unfished or lightly fished species may increase because of reduced predation (Bohnsack, 1982).

Several factors in addition to overfishing may have contributed to the decline in productivity of Jamaican reefs. Pollution can be severe in the coastal zone (Goodbody, 1989). There has been extensive reef damage from hurricanes in recent decades. Reduced coral production is associated with coral bleaching and coral overgrowth by algae, which may be exacerbated by the decline in herbivorous fishes, as well as by eutrophication.

Previous estimates of sustainable yield from the south Jamaican shelf may have been biased upward. An important assumption of the SPM is that the fishery is at equilibrium, such that the reported catch and effort are sustainable. The progressive decline of the fishery indicates that previous yields were not sustainable; therefore, estimates of MSY based on those catch and effort data were likely inflated.

Despite the progressive decline of the reef fish fauna on the south Jamaican shelf over recent decades, fishery assessments based on area-based SPM's indicated that the region was underutilized or only moderately exploited until as late as 1981 (Munro, 1978; Haughton, 1988). These analyses seem to have been confounded by combining data from the northern and southern Jamaican shelves without normalizing for the ~50% lower density of productive habitat on the southern shelf. The level of exploitation of the southern shelf relative to the northern shelf was therefore underestimated by ~50% (Fig. 5).

At present, the reef fishery on the south coast of Jamaica seems to be at the point of economic self-regulation (Gordon, 1954), such that effort has declined over the past decade owing to dramatically declining catch rates as a result of over fishing. In view of the general lack of opportunities in the Jamaican economy, an unmanaged reef fishery will remain heavily overfished and its productivity substantially reduced. Present landings from the southern shelf (0.5 t/km^2 of productive habitat) are approximately half the estimated potential MSY.

Our estimate of MSY (0.5 t/km^2 of shelf) is at the low end of estimates of maximum yield for reef fisheries in the Caribbean, which have generally ranged from 0.5 to 1.5 t/km^2 (Munro, 1983; FAO, 1985). Globally, estimates of sustainable yield from reef fisheries have ranged as high as 20 t/km^2, although these higher yields are generally from localized reefs rather than from entire shelf areas (Russ, 1991). Thus there may be a problem of standardization among studies.

In conclusion, we had only limited success in developing an area-based SPM for Jamaican and Belizean reef fisheries despite detailed surveys of catch and effort and estimation of the proportion of productive habitat in different areas. The difficulties seemed to be attributable to the nonequilibrium condition of the fisheries; the heterogeneous mix of species both within and between the two countries; the diversity of the fisheries that target a variety of spawning, sedentary, and possibly migratory animals; and to possible differences in productivity among sites. Thus the model's assumptions seem too restrictive to permit meaningful analysis of catch and effort data for such complex multispecies fisheries. Violation of the model's assumptions, particularly the nonequilibrium condition of the fishery, seems to have led to serious bias in previous analyses of sustainable yield and effort for the Jamaican fishery. More generally, these problems indicate that area-based multispecies SPM's should be used cautiously in guiding the future development of reef fisheries, unless the model's assumptions can be shown to be reasonably satisfied. Nonetheless, the changes in catch composition and the sharp declines in CPUE, yield, and estimated MSY in the Jamaican fishery over the past decade, despite declining fishing effort, are indicative of a severely overexploited fishery.

Acknowledgments

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Literature cited

Aiken, K. A., and M. Haughton.
1987. Status of the Jamaica reef fishery and proposals for its management. Proc. 38th Annu. Gulf and Caribbean Fisheries Inst. Meeting, p. 469–484.

Appeldoorn, R., and S. Meyers.
In press. Fisheries resources of Puerto Rico and Hispaniola. FAO Fish. Rep.

Bohnsack, J. A.
1982. Effects of piscivorous predator removal on coral reef fish community structure. *In* G. M. Cailliet and C. A. Simenstad (eds.), Gutshop '81: fish food habits studies. Washington Seagrant Publ., Univ. Washington, Seattle, WA.

Caddy, J. F., and S. Garcia.
1982. Production modelling without long data series. FAO Fish. Rep. 278 Suppl.:309–313.

FAO.
1985. Review of the state of the world fishery resources. FAO Fish. Circ. 710, Rev. 4, 61 p.

Fox, W. W.
1970. An exponential yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99:80–88.

Goodbody, I.
1989. Caribbean coastal management study: the Hellshire coast, St. Catherine, Jamaica. Marine Science Unit Research Rep. 2, 176 p.

Gordon, H. S.
1954. The economic theory of a common-property resource: the fishery. J. Pol. Econ. 62:124–142.

Gosse, P. H.
1851. A naturalist's sojourn in Jamaica. *In* D. B. Stewart (ed.), Gosse's Jamaica 1844–45, p. 3–47. Institute of Jamaica Publ., Kingston, Jamaica.

Haughton, M.
1988. An analysis of statistical data from the Jamaican inshore fisheries. *In* S. Venema, J. Moller-Christensen, and D. Pauly (eds.), Contributions to tropical fisheries biology. FAO Fisheries Rep. 389, p. 443–454.

Johannes, R. E.
1978. Traditional marine conservation methods in Oceania and their demise. Annu. Rev. Ecol. Syst. 9:349–364.

Koslow, J. A., F. Hanley, and R. Wicklund.
1988. Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. Mar. Ecol. Prog. Ser. 43:201–212.

Marten, G. G.
1979. Impact of fishing on the inshore fishery of Lake Victoria (East Africa). J. Fish. Board Can. 36:891–900.

Munro, J. L.
1978. Actual and potential fish production from the coralline shelves of the Caribbean Sea. FAO Fisheries Rep. 200:301–321.
1983. Caribbean coral reef fishery resources. ICLARM, Manila, Philippines, 276 p.

Nicholson, W., and L. Hartsuijker.
1982. The state of the fisheries resources of the Pedro Bank and south Jamaica shelf. FAO Fisheries Rep. 278 Suppl.:215–254.

Russ, G. R.
1991. Coral reef fisheries: effects and yields. *In* P. F. Sale (ed.), The ecology of fishes on coral reefs, p. 601–636. Academic Press, San Diego, CA.

Woodley, J. D., and E. Robinson.
1977. Field guidebook to the modern and ancient reefs of Jamaica. Third Int. Symposium on Coral Reefs, 33 p.

Abstract.—Commercial and scientific bottom longline catches of alfonsino, *Beryx splendens*, from seamounts off New Caledonia were sampled to study length-frequency distributions. A total of 14,674 fish were measured. CPUE of *Beryx splendens* on two seamounts is modelled in terms of length and depth. The data show that mean length increases with depth; this is well described by a bivariate normal model that estimates catch for a given seamount. In addition, the data show that mean length also varies with the depth of the top of seamounts; this is described by a recursive model that is designed to predict approximate catch for any seamount. The limitations of both models are discussed, particularly with regard to temporal variation.

Modelling the distribution of alfonsino, *Beryx splendens*, over the seamounts of New Caledonia

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Paul Marchal
René Grandperrin
Centre ORSTOM, BP A5, Noumea, New Caledonia

A bottom longline fishery operated on the seamounts of the Exclusive Economic Zone (EEZ) of New Caledonia from February 1988 to July 1991.[1] Three vessels were involved but only one vessel was operated at any given time. The fishing effort, which totalled 4,691,635 hooks, focused on five seamounts (B, C, D, J, and K) whose summits are located at depths ranging from 500 to 750 m (Fig. 1). The target species, alfonsino, *Beryx splendens*, accounted for 92% of the catch by weight. This species has a worldwide distribution, from the equator to the temperate latitudes, and is fished by bottom trawl or longline. Alfonsino generally occupies waters between 200 and 800 m, although it has been caught at depths of only 25 m and as deep as 1,240 m (Busakhin, 1982). Some authors have noted an increase in mean length with depth[2] (Yamamoto et al., 1978, Seki and Tagami, 1986), a trend which has been observed in other fishes (Heincke, 1913), particularly some deep-water demersal species[3, 4, 5] (Ralston and Williams, 1988). There have been few studies relating the size distribution of alfonsino to depth. The objective of this paper is to describe an approach for estimating the abundance of alfonsino by modelling its distribution in terms of fork length and depth of capture. A bivariate normal model describes this distribution for a given seamount and a recursive model predicts catch on any seamount.

Material and methods

Data

Alfonsino were captured with longline gear (Fig. 2). The main line, averaging 4,000 m, was held on the bottom by means of terminal anchors and regularly spaced heavy sinkers that delimited five equal line sections. During a fishing trip

[1] Grandperrin, R., and P. Lehodey. 1993. Etude de la pécherie de poissons profonds dans la zone économique de Nouvelle-Calédonie. Rapport final. Contrat de recherche ORSTOM / Territoire de Nouvelle-Calédonie. Nouméa: ORSTOM, Conv. Sci. Mer, Biol. Mar. 9, 321 p.

[2] Masuzawa, T., Y. Kurata, and K. Onishi. 1975. Results of group study on population of demersal fishes in water from Sagami Bay to the southern Izu Islands—population ecology of Japanese alfonsin and other demersal fishes. Japan Aquatic Resources Conserv. Assoc. Fish. Res. Paper 28, 105 p. [English translation held at Fisheries Research Centre Library, MAF, P.O. Box 297, Wellington].

[3] Brouard, F., and R. Grandperrin. 1985. Deep bottom fishes of the outer reef slope in Vanuatu. South Pacific Commission 17th Regional Technical Meeting on Fisheries, W P 12, 127 p.

[4] Clark, M. R., and K. J. King. 1989. Deep-water fish resources off the North Island, New Zealand: results of a trawl survey, May 1985 to June 1986. N.Z. Fish. Tech. Rep. 11, 55 p.

[5] Dalzell, P., and G. L. Preston. 1992. Deep reef slope fishery resources of the South Pacific. South Pacific Comm. Inshore Fish. Res. Project. Tech. Doc. 2, 299 p.

Manuscript accepted 31 March 1994.
Fishery Bulletin 92: 748–759.

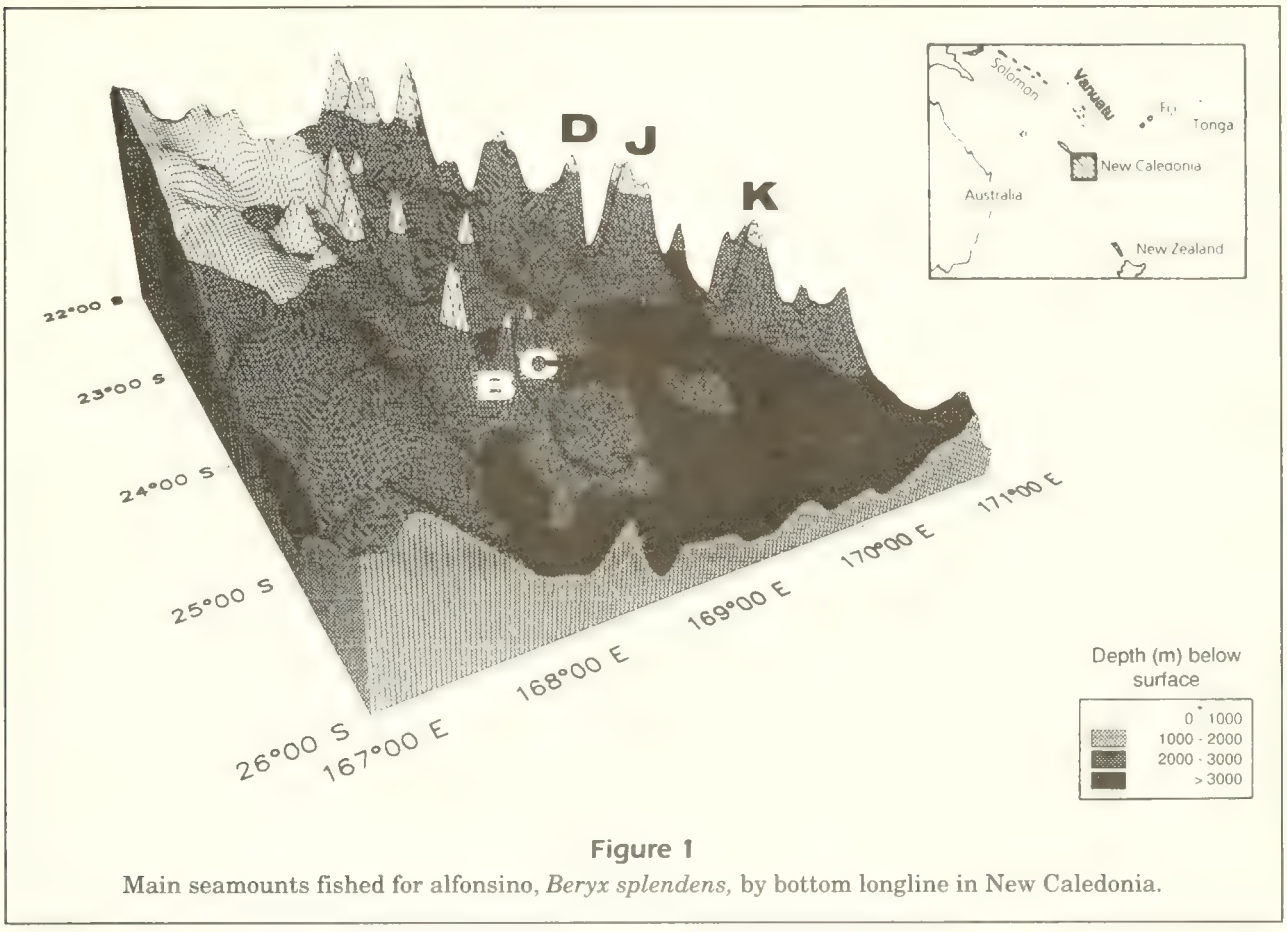

Figure 1

Main seamounts fished for alfonsino, *Beryx splendens,* by bottom longline in New Caledonia.

made by the longliner *Humboldt* from May to July 1991 over seamounts B, C, D, J, and K,[6] the depth profile of the bottom was recorded on an echosounder as the line was set. The position and the depth at the exact time the terminal anchors and intermediate sinkers were thrown overboard were also recorded. The longliner *Humboldt* was equipped with a Doppler sonar current indicator which provided current velocity and direction at three selected depths. Data recorded suggest that the current velocity rapidly decreased with depth (Fig. 3A) and that horizontal drift was probably minimal.[6] On 23 occasions over the total of 73 longline sets, the depth of the bottom was recorded at the time the buoy was grabbed at the beginning of retrieval. This depth was compared with the depth of the corresponding terminal anchor recorded when the line was set. Depth difference was less than 10 m for 74 % of the paired comparisons (Fig. 3B) which indicates that either the drift of the line during sinking was limited or the slope of the bottom was slight. Therefore, despite the lack of a maximum depth recorder to determine the actual depth of the main line (Somerton and Kikkawa, 1992), it was reasonable to assume that its configuration was similar to the depth profile indicated by the echosounder.

The estimated depth of the sinkers was used to allocate a mean value of depth of capture $\bar{d}_i = 1/2\ (d_i + d_{i+1})$ to all the fish caught on the same 800-m line section (Fig. 2). Ten meters, which is roughly half the length of the branch lines, was then added to each mean depth of capture d_i to correct for bias introduced by the fact that catches may occur at any hook level. Figure 3C gives the depth variation within each section. Eighty-one percent of the variation in depth is less than 15 m and 92% is within the 0–25 m range. This indicates that in most cases the longline was nearly horizontal with the bottom. Therefore, the allocation of a single depth of capture to all fish caught on the same line section seems reasonable, particularly as the depth of capture data were aggregated into 25-m depth classes for analysis. Dur-

[6] Lehodey, P. 1991. Mission d'observations halieutiques sur le palangrier *Humboldt*. Campagne de pêche du 30 mai au 12 juillet 1991, Nouméa. ORSTOM Rapp. Missions, Sci. Mer Biol., Mar. 8, 44 p.

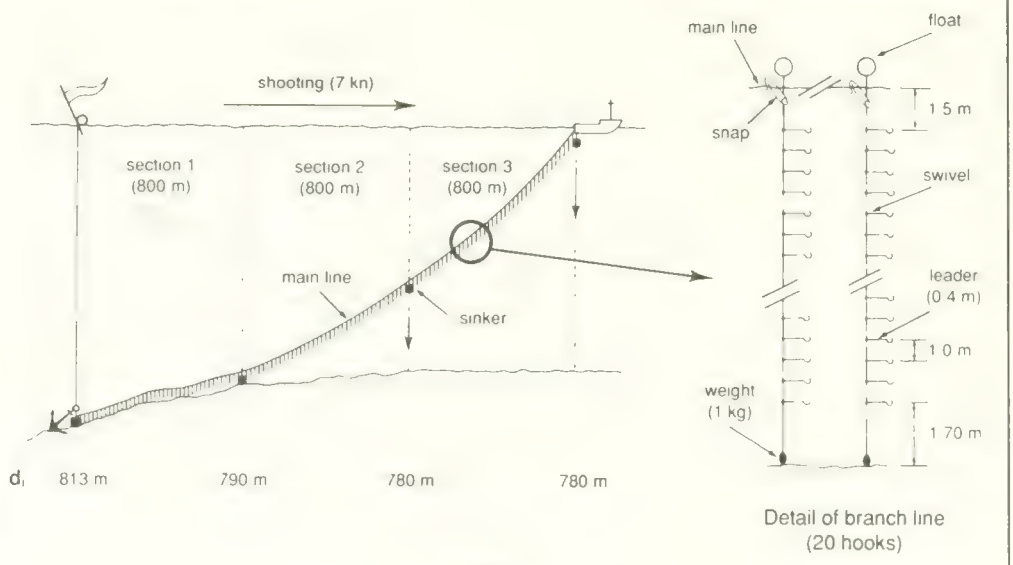

Figure 2

Longline gear employed from the longliner *Humboldt* during a set (15) on 7 June 1991 on seamount K (lat. 24°43'S; long. 170°06'E) and detail of a branch line. Main line is 4,000 m long and divided into five sections (each section has 840 hooks [42 branch lines × 20 hooks] and is 800 m long). d_i depth recorded on the echosounder at time t_i when sinker was thrown overboard; $d_i = 1/2\ (d_i + d_{i+1}) + 10$ = mean depth of capture allocated to all fish hooked on section i.

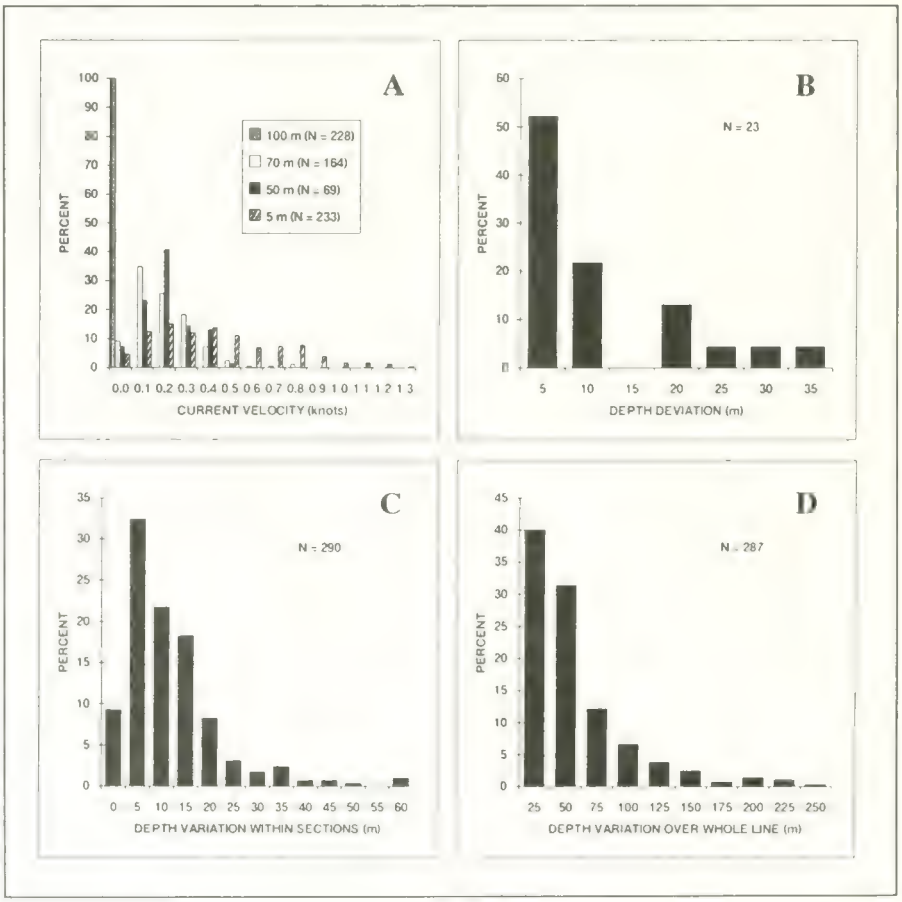

Figure 3

Measurements taken to assess the deviation between the depth profile recorded on the echosounder and the actual configuration of the longline on the bottom: (**A**) current velocity from the Doppler sonar current indicator recorded at different depths during the settings of the longline by the *Humboldt* (n=694 current measurements); (**B**) deviations between the depth of the terminal anchor recorded when the line was set and the depth of the bottom recorded at the time the corresponding buoy was grabbed at the begining of retrieval (n=23 sets); (**C**) depth variations within sections recorded during the fishing cruise carried out by the longliner *Humboldt* (n=290 line sections of 800 m each); (**D**) depth variations (differences between maximum and minimum depths) for the whole line recorded during the fishing cruises carried out by the longliners *Hokko Maru* and *Fukuju Maru* (n=287 longlines of 4,000 m).

ing two other commercial cruises conducted by the longliners *Hokko Maru* and *Fukuju Maru*, observers recorded the maximum and minimum depths reached by the longline[7, 8] (Fig. 3D).

Fork length (FL) was measured on a total of 14,674 alfonsino. During the commercial fishing trips, fish to be measured were randomly sampled from each set. When there were only a few fish, they were all measured. As the samples varied in size between sets, the length-frequency distribution of all the alfonsino caught was estimated by multiplying the number in the sample by the ratio of the total number of alfonsino caught to the total number of alfonsino measured for each longline set. During several scientific cruises all of the fish were measured.[1] Because all the depth zones were not sampled in the same way, catch per unit of effort (CPUE=number of fish caught per 100,000 hooks) was taken as the abundance index.

The data collected during the *Humboldt* cruise was used to model the distribution of CPUE in terms of length and depth over seamounts. The models were validated with data generated by the scientific cruises and with data collected on board the two additional commercial boats, *Hokko Maru* and *Fukuju Maru*. These commercial data are less precise because only maximum and minimum longline depths were recorded.

Preliminary data analysis

Table 1 shows the mean fork length by depth zone for each seamount sampled during the *Humboldt* cruise. This table suggests a significant increase in mean length with depth on each seamount. In order to model this increase, the data must be as representative as possible of the fish population over its depth range. For this reason, only data recorded for seamounts B and J were used for modelling the increase in length with depth.

[7] Anonymous. 1988. Rapport de la campagne de pêche à la palangre profonde dans la zone économique de la Nouvelle-Calédonie. *Hokko Maru* 107: février–mai 1988. Territoire de Nouvelle-Calédonie, Service Territorial de la Marine Marchande et des Pêches Maritimes, 57 p.

[8] Laboute, P. 1989. Mission d'observation halieutique sur le palangrier japonais *Fukuju Maru* du 21 nov. au 12 déc. 1988, Nouméa. ORSTOM Rapp. Missions, Sci. Mer Biol. Mar. 2, 15 p.

Table 1

Analysis of variance and multiple comparisons of mean fork length (cm) of alfonsino, *Beryx splendens*, sampled on five seamounts during the *Humboldt* fishing cruise (sample size in parentheses).

Water depth of top (m)	Seamount B [502 m]	C [560 m]	J [630 m]	D [630 m]	K [710 m]	α*
< 525	33.27 (52)					
525–549	34.90 (665)					
550–574	37.11 (635)	34.72 (405)				0.0001
575–599	38.08 (82)	36.78 (1083)				0.0007
600–624	40.39 (125)	38.95 (74)	35.23 (262)			0.0001
625–649			36.24 (462)			
650–674			37.55 (913)	35.73 (138)		0.0001
675–699			38.16 (115)	35.54 (295)		0.0001
700–724						
725–749			40.60 (205)			
750–774					38.21 (309)	
775–799					39.90 (308)	
+ 800					40.57 (53)	
α*	0.0001	0.0001	0.0001	0.4979	0.0001	

* If α is less than 0.05 then the hypothesis that the means are the same in all classes is rejected. All individual means were compared pairwise with the multiple comparison test of Tukey-Kramer (in SAS, 1988) The shaded boxes indicate that the two included means are not significantly different at the 0.05 level.

CPUE distributions by size class and depth zone over seamounts B and J from the *Humboldt* are shown in Figure 4. A preliminary examination of the data revealed that they fitted portions of curves conforming to a normal distribution. It was therefore assumed that for a given seamount the CPUE, in terms of length and depth, was distributed over a surface described by a bivariate normal distribution function delimited by the maximum and minimum of lengths and depths sampled. This assumption is the basis of the first modelling exercise ("bivariate normal model").

Table 1 also shows that, for a given absolute depth, mean length significantly decreases as the depth of the top of the seamount increases. This decrease suggests that the length distribution depends both on the absolute depth (in relation to the sea surface) and on the depth of the top of the seamount. Consequently, the bivariate normal model constructed for a given seamount may not be applicable to other seamounts whose summits lie at different depths. It is therefore necessary to construct a more general model (referred to as the "recursive model") which would predict extrapolated estimates of CPUE over any seamount by taking into account both the absolute depth of the water column and the depth of the top of the seamount. Temporal validation of these two models requires data that were not used during model construction but were collected in the same area at different periods. Data collected on board RV *Alis* and the fishing vessels *Hokko Maru* and *Fukuju Maru* were used for model validation.

Modelling method

Bivariate normal model In the bivariate normal model, CPUE by length and depth are calculated on the basis of a bivariate normal distribution defined by the density function (1)

$$B(x_l,x_d) = \frac{1}{2\pi\sigma_l\sigma_d\sqrt{1-\rho^2}} \exp\left\{\frac{1}{2(1-\rho^2)}\left[\left(\frac{x_l-\mu_l}{\sigma_l}\right)^2 - 2\rho\frac{(x_l-\mu_l)(x_d-\mu_d)}{\sigma_l\sigma_d} + \left(\frac{(x_d-\mu_d)}{\sigma_d}\right)^2\right]\right\}, \quad (1)$$

where x_l is the length, x_d is the depth, μ_l is the mean length, σ_l is the standard deviation of length, μ_d is the mean depth, σ_d is the standard deviation of depth, and ρ is the regression coefficient of length on depth. Because sampling of the seamounts is limited upwards by their summit (D_s) and downwards by the maximum depth accessible with the bottom longline (D_a), CPUE distributions will be modelled by a portion of the bivariate normal distribution (2)

$$\begin{cases} \mathrm{CPUE}_{est}(x_l,x_d) = 0 & \text{for } x_d > D_a \text{ or } x_d < D_s \\ \mathrm{CPUE}_{est}(x_l,x_d) = \lambda\, B(x_l,x_d) & \text{for } D_s \le x_d \le D_a \end{cases} \quad (2)$$

where λ represents the theoretical cumulative CPUE estimated over the field of definition of the entire bivariate normal distribution. The parameters λ, μ_l, σ_l, μ_d, σ_d and ρ were estimated by a nonlinear regression by using an iterative algorithm for sum of squares errors (SSE) minimization (SAS, 1988).

Recursive model The recursive model should allow estimation of alfonsino CPUE by size class for seamounts for which no data are available except the depth of their summit. The size structure variation shown in Table 1 should be taken into account in the development of this model, i.e. 1) for a given seamount, mean length increases with depth and 2) for a given depth zone, mean length decreases as the depth of the top of the seamount increases. In theory, the distribution of a population of alfonsino over any seamount could then be taken as the superposition of the distributions of two subpopulations: one population would be influenced only by the absolute depth while the other would be influenced by the depth of the top of the seamount. This model attempts to explain how the fish population of a given seamount would in theory redistribute itself if it were to migrate and settle on another seamount. Consider a hypothetical population whose cumulative CPUE (λ_o) by length and depth is distributed over its seamount of origin according to a bivariate normal distribution function of unknown μ_l, σ_l, μ_d, σ_d, and ρ parameters. For the estimation of these parameters, the top of the hypothetical original seamount will be assumed to be exactly level with the sea surface in order to include the entire depth zone that could be inhabited by alfonsino. The new CPUE distribution on seamounts j, j+1, etc. . . (Fig. 5) will depend on the initial parameters of the distribution over the original seamount as well as on parameter p, the probability that the fish will redistribute according to absolute depth, and (1–p), the probability that the fish will redistribute according to the depth of the top of the seamount. At each "leap" to a deeper seamount (from j to j+1), the subpopulation inhabiting a given depth zone D_t will split into two groups: one group will stay in the same depth zone D_t with a probability p (or will migrate elsewhere if this zone is no longer available on the new seamount) and the other

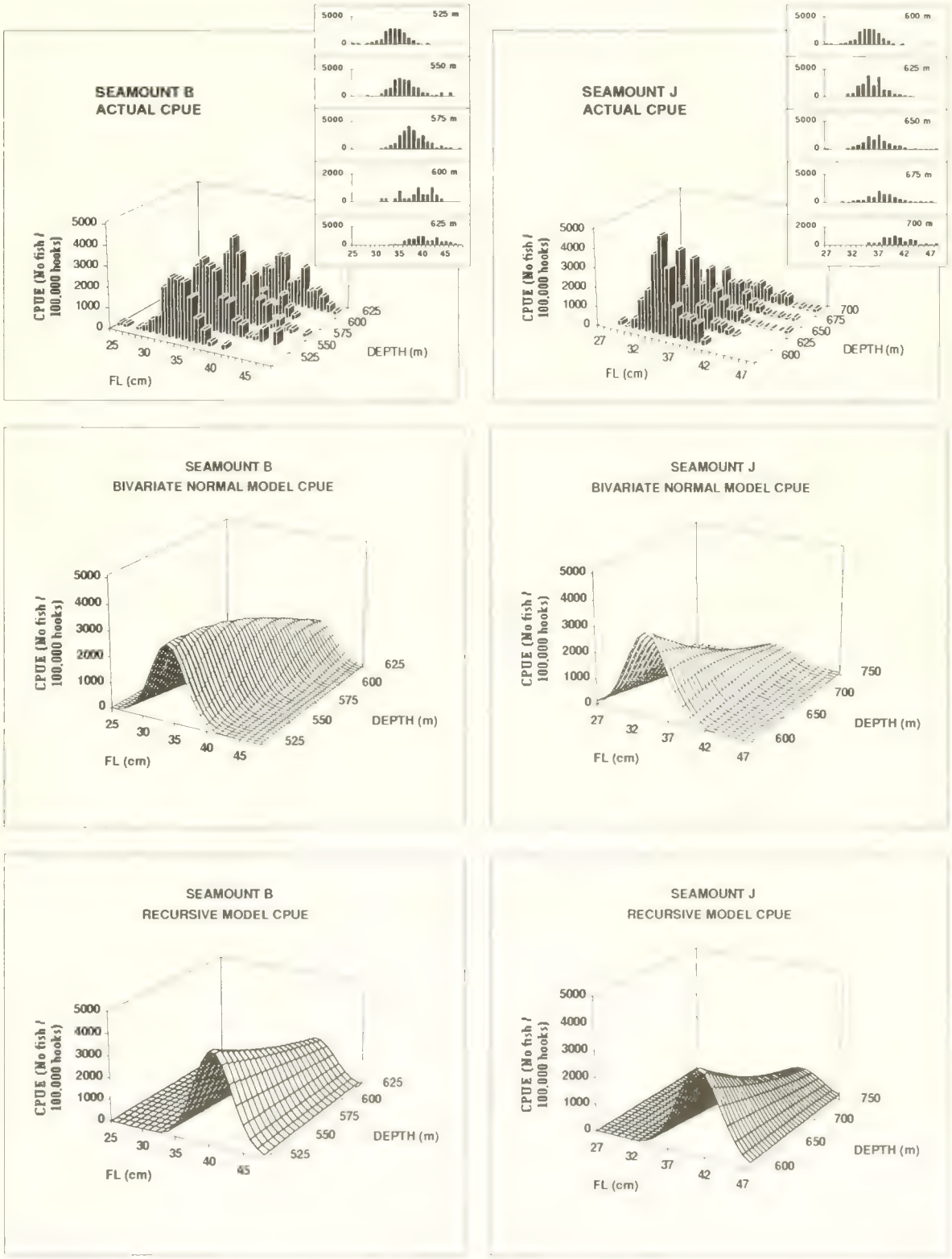

Figure 4

Actual CPUE for alfonsino, *Beryx splendens*, by fork length (cm) and depth (m), recorded on seamounts B and J during the fishing cruise carried out by the longliner *Humboldt*, and predicted CPUE from the bivariate normal model and the recursive model.

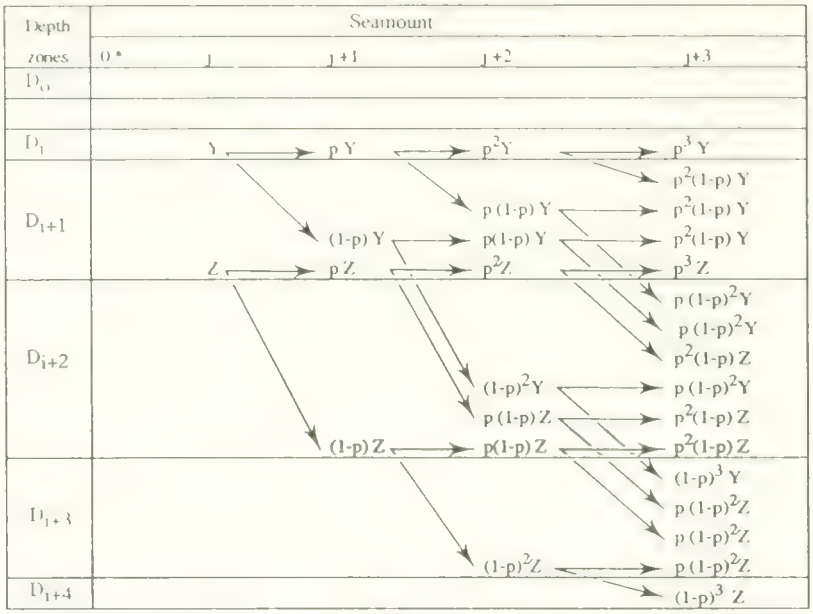

Figure 5

Changes in distribution of alfonsino, *Beryx splendens*, according to the recursive model of two subpopulations *Y* and *Z* that migrate from a seamount j to deeper seamounts $j+1, j+2, j+3$. *Y*=subpopulation distributed on a seamount *j* at absolute depth D_i; *Z*=subpopulation distributed on a seamount *j* at absolute depth D_{i+1}; *p*=probability that fish will redistribute according to absolute depth; 1–*p*=probability that fish will redistribute according to the depth of the top of the seamount; *=original seamount.

group will move down to zone D_{i+1} with a probability 1–*p* (Fig. 5). Thus, it is possible to determine the CPUE ($X_{i,j,k}$) for the population of a depth zone D_i, on a seamount *j*, for a size class *k* in terms of the subpopulations of zones D_i and D_{i-1} on the higher-level seamount *j*–1. This is expressed as follows:

$$X_{i,j,k} = pX_{i-1,j-1,k} + (1-p)X_{i,j-1,k}. \quad (3)$$

Specifically, if *p*=0, CPUE is distributed solely according to the depth of the top of the seamount and if *p*=1, it is distributed solely according to the absolute depth. If the parameters λ_o, μ_l, σ_l, μ_d, σ_d, ρ, and *p*, estimated from a known seamount length-depth distribution are known, it is possible to calculate all the CPUE ($X_{i,j,k}$) values for any seamount *j* (deeper or shallower), depth zone D_i and size class *k*. The foregoing seven parameters can be estimated by minimizing the SSE between the CPUE recorded on one of the best sampled seamounts (B or J) and the CPUE estimated by Equation 3. This estimation is performed by a nonlinear regression (SAS, 1988).

Results

Bivariate normal model

Application of a bivariate normal model implies that mean length can be deduced from depth by a linear regression weighted by the CPUE $\bar{x}_i = a x_d + b$ where a and b are constants). The results of this regression for seamounts B and J show mean length and depth to be significantly correlated (Table 2). Consequently, the bivariate normal model can be tested for each of these seamounts.

The parameters of the bivariate normal model were calculated separately for seamounts B and J (Table 3). The determination coefficient,[9] R^2, for seamounts B and J respectively equals 0.87 and 0.93. The residual analysis was carried out to test the fit of the model to the data from the *Humboldt* cruise on seamounts B and J. The results show the residuals are

[9] $R^2 = \left[\sum (Y - \bar{Y})^2 - \sum (Y - \hat{Y})^2\right]$ with Y = CPUE.

Table 2

Bivariate normal model: CPUE – weighted linear regression of length of alfonsino, *Beryx splendens*, on depth.

Seamount	No. of fish measured	Min. depth (m)	Max. depth (m)	ρ	α	H_0: $r = 0$	a	b
B	1,557	516	615	0.549	< 0.0001	rejected	0.063	0.037
J	1,957	606	761	0.486	< 0.0001	rejected	1.251	13.122

ρ = regression coefficient.
α = significance probability of the regression under the null hypothesis that the statistic is zero.
H_0 = null hypothesis i.e. length and depth are independent; if $\alpha < 0.05$, H_0 is rejected.
a and b = parameters of the linear regression.

satisfactory; in particular, the residuals are centered on zero, are not correlated with the length and depth variables, and have a constant variance (Table 4; Fig. 6). These characteristics indicate a good fit of the bivariate normal model to the data as demonstrated by comparison of actual and predicted CPUE (Fig. 4).

Extrapolation of the model to the data not used in the modelling exercise is unsatisfactory because the mean value of the residuals is not centered on zero for the *Fukuju Maru* data and because the residuals are correlated with the length variable for the RV *Alis* data and with the depth variable for the *Hokko Maru* data (Table 4; Fig. 6). This suggests the existence of factors affecting the population's distribution not accounted for by the model.

Table 3

Bivariate normal model: predicted parameters for seamounts B and J. SD=Standard deviation.

	Seamount and number of fish measured			
	B 1,557		J 1,957	
Parameters	Estimation	SD	Estimation	SD
λ	3.66×10^6	0.85×10^6	0.5×10^9	4.5×10^9
μ_l	35.22	0.96	12.0	52.0
μ_d	542.87	14.49	−123.1	1,666.7
σ_l	5.31	1.01	8.8	9.6
σ_d	71.07	17.04	272.5	317.1
ρ^2	0.75	0.10	0.9	0.2

λ=theoretical cumulative CPUE.
μ_l=mean length (cm).
μ_d=mean depth (m).
σ_l=standard deviation of length.
σ_d=standard deviation of depth.
ρ^2=regression coefficient of length on depth.

Recursive model

The parameters of the recursive model were estimated separately for seamounts B and J. The deter-

Table 4

Bivariate normal model: results of analysis of residuals (ε) for fit control and temporal validation of the model for seamounts B and J.

	Cruise	Seamount	No. of fish measured	α_1	$H_0: \bar{\varepsilon} = 0$	α_2	$H_0: \rho_1 = 0$	α_3	$H_0: \rho_2 = 0$
Fit control	*Humboldt*	B	1,557	0.289	not rejected	0.153	not rejected	0.149	not rejected
	Humboldt	J	1,957	0.068	not rejected	0.061	not rejected	0.431	not rejected
Temporal validation	*Hokko Maru*	B	2,840	0.262	not rejected	0.601	not rejected	<0.0001	rejected
	RV *Alis*	B	1,688	0.908	not rejected	0.016	rejected	0.391	not rejected
	Fukuju Maru	J	4,320	0.0002	rejected	0.265	not rejected	0.284	not rejected

$H_0: \bar{\varepsilon} = 0$. The mean value of the deviations between estimated and observed CPUE is 0. If α_1 is <0.05, H_0 is rejected.
ρ_1= regression coefficient of ε on length.
ρ_2=regression coefficient of ε on depth.
H_0:$\rho_1 = 0$. If α_2 is< 5%, H_0 is rejected.
H_0:$\rho_2 = 0$ If α_3 is < 5%, H_0 is rejected.

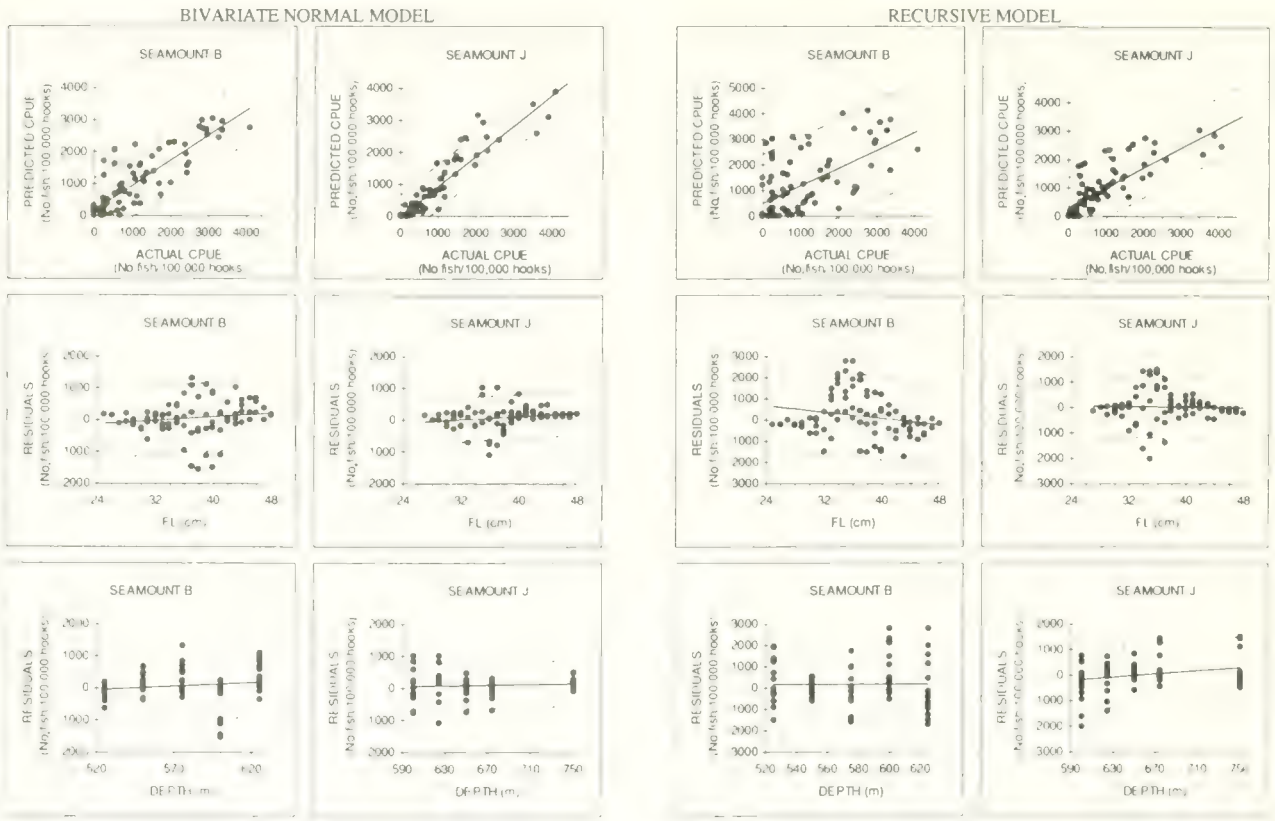

Figure 6

Bivariate normal model and recursive model for seamounts B and J: distribution of predicted CPUE of alfonsino, *Beryx splendens*, in relation to actual CPUE and distributions of residuals in relation to length (cm) and depth (m). Dotted lines delimit the confidence interval at α=0.05.

Table 5

Recursive model: estimated parameters of the distribution of CPUE on the hypothetical original seamount calculated from seamount J data. SD = standard deviation.

Parameters	Estimation	SD
	22.86	91.3
	−66.17	499.9
	5.98	16.5
	30.27	99.2
	0.87	0.70
	0.09	0.04
	1.15×10^{8}	2.33×10^{8}

σ_d=standard deviation of depth.

p=probability that fish will redistribute according to absolute depth

λ_{th}=theoretical cumulative CPUE

mination coefficient, R^2, calculated for seamount J equals 0.82, while for seamount B it equals 0.69. Therefore, the parameters estimated for seamount J were used in the model (Table 5). The residuals resulting from fitting the model to data from the *Humboldt* cruise on seamount J are satisfactory; in particular, they are centered on zero and are not correlated with the studied variables (Table 6; Fig. 6). These features indicate a good fit of the recursive model to the data as demonstrated by comparison of actual and predicted CPUE for seamount J (Fig. 4). It is interesting to note the low value of p (close to 0.1 as shown in Table 5), which indicates that the seamount top depth parameter has greater impact on the length distribution than does the absolute depth parameter.

Spatial validation was carried out for seamount B from the data collected during the *Humboldt* cruise (Table 6). The residuals are centered on zero and not correlated with the length and depth variables. However, since their variance is not constant (Fig. 6) and

Table 6

Recursive model: results of analysis of residuals (ε) for fit control and validation of the model for seamounts B and J.

	Cruise	Seamount	No. of fish measured	α_1	$H_0 : \bar{\varepsilon} = 0$	α_2	$H_0 : \rho_1 = 0$	α_3	$H_0 : \rho_2 = 0$
Fit control	*Humboldt*	J	1,957	0.87	not rejected	0.85	not rejected	0.06	not rejected
Spatial validation	*Humboldt*	B	1,557	0.13	not rejected	0.06	not rejected	0.99	not rejected
Temporal validation	*Hokko Maru*	B	2,840	0.15	not rejected	0.76	not rejected	<0.0001	rejected
	RV *Alis*	B	1,688	0.01	rejected	0.005	rejected	0.35	not rejected
	Fukuju Maru	J	4,301	0.007	rejected	0.67	not rejected	0.08	not rejected

$H_0 : \bar{\varepsilon} = 0$. The mean value of the residuals is 0. If α_1 is <5%, H_0 is rejected.
ρ_1 = regression coefficient of ε on length
ρ_2 = regression coefficient of ε on depth.
$H_0 : \rho_1 = 0$. If α_2 is <5%, H_0 is rejected.
$H_0 : \rho_2 = 0$. If α_3 is <5%, H_0 is rejected.

since the standard deviations of the parameters are high (Table 5), spatial extrapolation of the model to seamount B is rather crude as demonstrated by comparison of actual and predicted CPUE (Fig. 4).

Temporal validation was carried out on data from the *Fukuju Maru* and RV *Alis* fishing on seamounts B and J (Table 6). It is unsatisfactory because the mean values of the residuals are not centered on zero and the residuals are correlated with the length variable for the RV *Alis* data and with the depth variable for the *Hokko Maru* data (Fig. 6). As with the bivariate normal model, this suggests the existence of factors not accounted for by the model.

Discussion

Alfonsino length structure variation observed over the seamounts of New Caledonia is similar to that noted in Japan[2] and in New Zealand[10] (Massey and Horn, 1990) where it was assigned to age-specific migrations. In Japan, it was noted that alfonsino move south as they grow,[2] young fish predominate over some seamounts and old fish predominate over other seamounts. In New Caledonia, age segregation over the seamounts is so marked that it has been possible to describe it mathematically.

The bivariate normal and recursive models appear to be complementary. The bivariate normal model provides an instantaneous picture of alfonsino population distribution on a given seamount; it provides good CPUE estimates provided a sufficient amount of length and depth data are available. The recursive model takes into account the dynamic nature of the population's distribution as it allows the extrapolation of CPUE obtained for one seamount to seamounts that were not sampled. It allows preliminary population estimation of unexploited stocks. Depending on current economic parameters, the model might be used to indicate the depths at which fishing is most economic. Once a fishery is operational, more refined data will be available, which will enable the bivariate normal model to be applied and stock management parameters defined for each of the seamounts fished.

The poor results obtained for the temporal validation could be due to poor precision of the depth data collected from the longliners *Hokko Maru* and *Fukuju Maru*. Also, neither of the models incorporate a time factor. The data were collected from cruises carried out in different years and in different seasons. Hence, it is unlikely that conditions remained stable, particularly with regard to exploitation history, reproductive behavior, or long-term climatic variations.

Fishing methods and strategies were not modified during the fishing period considered. Therefore, the catches are probably representative of the standing stock of alfonsino within the size limits determined by the selectivity of the fishing gear. Since the daily observation window did not change, vertical trophic migrations would seem unlikely to contribute to the observed variability. With regard to sex as a source of variability, although the mean length of females exceeds that of males[11] (Kotlyar, 1987; Massey and

[10] Horn, P. L., and B. R. Massey. 1989. Biology and abundance of alfonsino and bluenose off the lower east coast, North Island, New Zealand. N. Z. Fish. Tech. Rep. 15, 31 p.

[11] Lehodey, P. 1994. Les monts sous-marins de Nouvelle-Calédonie et leurs ressources halieutiques. Thèse de doctorat de l'Université Française du Pacifique, 398 p.

Horn, 1990), Humphreys et al. (1984) have shown that sexual dimorphism is not responsible for the existence of different size groups of alfonsino. Marked declines in CPUE are observed in the Southern Hemisphere during summer. This season corresponds to the alfonsino breeding period in New Caledonian waters.[11] The summer decline in catch rate could be due to breeding migrations drawing the fish to spawning grounds that are different from the fishing grounds[2] (Chikuni, 1971) or to changes in vulnerability to the gear owing to seasonal physiological or behavioral changes (Ricker, 1980). Data used to build the models were collected on board the *Humboldt* during the winter season. Data used to validate the models were collected on board *Fukuju Maru* and *Hokko Maru* at the beginning and end of the warm season and during six scientific cruises, five of which were carried out in summer. This suggests that reproductive seasonality might be a factor in the poor temporal validation of the models.

Other sources of temporal variation might be related to the environment. The ocean habitat of alfonsino is not affected by continental influences but is subject to hydrological fluctuations affecting the deep-water masses. Some of these influences are of short period such as internal waves and tidal currents (Eriksen, 1985; Roden, 1987), whereas others recur at longer intervals such as seasonal variations in ocean currents and multi-annual hydroclimatic anomalies of the El Niño Southern Oscillation (ENSO) (Delcroix and Hénin, 1989). Such fluctuations might have an impact on alfonsino stock structure, either at the recruitment stage (survival and dispersal of eggs and larvae) or by modification of the behavior of adults (migrations from one seamount to another). However, it is difficult to demonstrate the effect of these fluctuations on the presence and catchability of fish. It is even more difficult to explain the very large differences in fishery productivity observed between seamounts of identical depth, located only a few dozen miles apart and appearing to have the same hydrological environment. Seafloor topography and bottom type might account for these differences, but other hypotheses can be postulated, some based on the existence of a low-energy hydrothermalism (Rougerie and Wauthy, 1990) and others on a hydrological anomaly called "Taylor's column," which could enhance species sedentarity (Royer, 1978; Genin and Boehlert, 1985; Roden, 1987; Dower et al., 1992; Sime-Ngando et al., 1992). Fluctuations in intensity of this anomaly, or its disappearance, could also be responsible for the variations in productivity observed over time over a given seamount (Boehlert and Genin, 1987). These unknown environmental fluctuations cause problems in the interpretation of results from exploratory and commercial fishing cruises carried out over seamounts. The data collected at a given location constitute an instant picture of a stock whose abundance is likely to vary, irrespective of fishing effort, as a result of unknown environmental variations. In other words, the fertility of the seamounts could vary quite unpredictably over the history of a fishery. Consequently, modelling the distribution of a stock should be confined to a relatively small temporal sampling scale.

Conclusion

The bivariate normal model and the recursive model provide complementary interpretations of length distribution in terms of depth of alfonsino fished on the seamounts of New Caledonia by the bottom longline fishery. They could be useful for the proper management of fisheries over seamounts, where stocks are known to be vulnerable (Sasaki, 1986) because of the limited habitat afforded by seamounts and the slow growth rate of deep-water species. However, it would appear that annual or seasonal factors, in particular those which account for recruitment fluctuations and behavioral changes linked to reproduction, will need to be incorporated into the models before they can be generalized. A better understanding of the functioning of the ecosystems concerned would also assist in establishing the limits of generalization, particularly with regard to depth and area inhabited by alfonsino. These models could possibly be adapted to other deep-water species such as certain snappers and groupers.

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Literature cited

Boehlert, G. W., and A. Genin.
1987. A review of the effects of seamounts on biological processes. *In* B. H. Keating, P. Fryer, R. Batiza, and G. W. Boehlert (eds.), Seamounts, islands and atolls. Geophysical Monograph. 43:319–334.

Busakhin, S. V.
1982. Systematics and distribution of the family Berycidae (Osteichthyes) in the world ocean. J. Ichthyol. 22 (6):1–21.

Chikuni, S.
1971. Groundfish on the seamounts in the North Pacific. Bull. Jpn. Soc. Fish. Oceanogr. 19:1–14. [English translation by K. Tatara, 1972, Fish. Res. Board Can., Translation no. 2130, 12 p.]

Delcroix, T., and C. Hénin.
1989. Mechanisms of subsurface thermal structure and sea surface thermohaline variabilities in the southwestern tropical Pacific during 1975–85. J. Mar. Res. 47: 777–812.

Dower, J., H. Freeland, and K. Juniper.
1992. A strong biological response to oceanic flow past Cobb Seamount. Deep-Sea Res. 39 (78): 1139–1145.

Eriksen, C. C.
1985. Implications of ocean bottom reflexion for internal wave spectra and mixing. J. Phys. Oceanogr. 15:1145–1156.

Genin, A., and G. W. Boehlert.
1985. Dynamics of temperature and chlorophyll structures above a seamount: an oceanic experiment. J. Mar. Res. 43:907–924.

Heincke, F.
1913. Untersuchungen über die Scholle, Generalbericht I. Schollenfischerei und Schonmassregeln. Vorläufige Kurze Übersicht über die wichtigsten Ergebnisse des Berichts. Rapp. P-Verb. Cons. Int. Explor. Mer 16:1–70.

Humphreys, R. L., Jr., D. T. Tagami, and M. P. Seki.
1984. Seamount fishery resource within the southern Emperor–northern Hawaiian Ridge area. *In* R. W. Grigg and K. Y. Tanoue (eds.), Proceedings of the symposium on resource investigations in the northwestern Hawaiian Islands, 25–27 May, 1983, Vol. 1, p. 283–327.

Kotlyar, A. N.
1987. Age and growth of alfonsino, *Beryx splendens*. J. Ichthyol. 27 (2):104–111.

Massey, B. R., and P. L. Horn.
1990. Growth and age structure of alfonsino (*Beryx splendens*) from the lower east coast, North Island, New Zealand. N. Z. J. Mar. Freshwater Res. 24 (1):121–136.

Ralston, S. V., and H. A. Williams.
1988. Depth distributions, growth, and mortality of deep slope fishes from the Mariana Archipelago. NOAA Tech. Mem. NMFS-SWFC-113, 47 p.

Ricker, W. E.
1980. Calcul et interprétation des statistiques biologiques des populations de poissons. Bull. Fish. Res. Board Can. 191 F, 409 p.

Roden, G. I.
1987. Effect of seamounts and seamounts chains on ocean circulation and thermohaline structure. *In* B. H. Keating, P. Fryer, R. Batiza, and G. W. Boehlert (eds.), Seamounts, islands and atolls. Geophysical Monograph. 43:335–354.

Rougerie, F., and B. Wauthy.
1990. Les atolls oasis. La Recherche 223:832–842.

Royer, T. C.
1978. Ocean eddies generated by seamounts in the North Pacific. Science 199:1063–1064.

SAS (Statistical Analysis System).
1988. SAS/STAT user's guide, release 6.03 ed. SAS Institute Inc., Cary, NC, 1028 p.

Sasaki, T.
1986. Development and present status of Japanese trawl fisheries in the vicinity of seamounts. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (eds.), The Environment and resources of seamounts in the North Pacific. NOAA Tech. Rep. NMFS 43: 21–30.

Seki, M. P., and D. T. Tagami.
1986. Review and present status of handline and bottom longline fisheries for alfonsin. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (eds.), Environment and resources of seamounts in the North Pacific. NOAA Tech. Rep. NMFS 43:31–35.

Sime-Ngando, T., K. Juniper, and A. Vesina.
1992. Ciliated protozoan communities over Cobb Seamount: increase in biomass and spatial patchiness. Mar. Ecol. Prog. Ser. 89: 37–51.

Somerton, D. A., and B. S. Kikkawa.
1992. Population dynamics of pelagic armorhead *Pseudopentaceros wheeleri* on Southeast Hancock Seamount. Fish. Bull. 90:756–769.

Yamamoto, S., K. Ishii, S. Sasaki, and T. Meguro.
1978. Outlines of fisheries investigation on the Emperor seamounts by the R.V. *Hokusei Maru* in 1977 and some technical problems. Bull. Jpn. Soc. Fish. Oceanogr. 33:56–64.

Spawning and early life history of white sturgeon, *Acipenser transmontanus*, in the lower Columbia River

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Abstract.—Spawning and early life history of white sturgeon, *Acipenser transmontanus*, were studied in the lower Columbia River downstream from Bonneville Dam from 1988 through 1991. From white sturgeon egg collections, we determined that successful spawning occurred in all four years and that the estimated spawning period each year ranged from 38 to 48 days. The spawning period extended from late April or early May through late June or early July of each year. Spawning occurred primarily in the fast-flowing section of the river downstream from Bonneville Dam, at water temperatures ranging from 10 to 19°C. Freshly fertilized white sturgeon eggs were collected at turbidities ranging from 2.2 to 11.5 nephelometric turbidity units (ntu), near-bottom velocities ranging from 0.6 to 2.4 m/s, mean water column velocities ranging from 1.0 to 2.8 m/s, and depths ranging from 3 to 23 m. Bottom substrate in the river section where freshly fertilized eggs were most abundant was primarily cobble and boulder. White sturgeon larvae were collected from river kilometer (rkm) 45 to rkm 232, suggesting wide dispersal after hatching. Larvae were collected as far downstream as the upper end of the Columbia River estuary, which is a freshwater environment. Young-of-the-year (YOY) white sturgeon were first captured in late June, less than two months after spawning was estimated to have begun. Growth was rapid during the first summer; YOY white sturgeon reached a minimum mean total length of 176 mm and a minimum mean weight of 30 g by the end of September. Young-of-the-year white sturgeon were more abundant in deeper water (mean minimum depth ≥12.5 m) of the lower Columbia River. The results indicate that a large area of the lower Columbia River is used by white sturgeon at different life history stages.

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White sturgeon, *Acipenser transmontanus*, is the largest of all North American sturgeon species and is found along the west coast of North America from the Aleutian Islands, Alaska, to Monterey, California (Scott and Crossman, 1973). Although this species is generally anadromous (Scott and Crossman, 1973), some populations in the Columbia River Basin are landlocked because of dam construction or natural barriers (Cochnauer et al., 1985; Beamesderfer et al.[1]).

Historically, white sturgeon were abundant in the Columbia River (Oregon and Washington) and in the late 1800's supported an intense commercial fishery. Commercial catches peaked in 1892, when more than 2.4 million kg were landed (Craig and Hacker, 1940). After 1892, catches declined, and by 1899 the annual catch was less than 33,250 kg. Annual catches during the early 1900's were less than 104,930 kg (Craig and Hacker, 1940).

White sturgeon populations in the Columbia River, particularly the one downstream from Bonneville Dam (the lowest dam at river kilometer [rkm] 234), have recovered sufficiently from the overfishing to support important recreational and commercial fisheries. The population of white sturgeon in the lower Columbia River, which extends from the mouth of the river to Bonneville Dam, is one of the largest in the world. From 1984 through 1988, the combined recreational and commercial catch in this area was at least 50,000 fish annually (Wash. Dep. Fisheries and Oregon Dep. Fish and Wildlife[2]). During 1992, estimated catches of white sturgeon for recreational and commercial fisheries were 40,100 and 6,200 fish, respectively (Melcher and King[3]). Presently, white sturgeon is the principal recreational fish in the Columbia River downstream from Bonneville Dam (Melcher and King[3]).

[1] Beamesderfer, R. C., T. A. Rien, C. A. Foster, and A. L. Ashenfelter. 1990. Report A. *In* A. A. Nigro (ed.), Status and habitat requirements of white sturgeon populations in the Columbia River downstream from McNary Dam, p. 6–37. Ann. Rep. to Bonneville Power Admin. (Project 86-50) by Oreg. Dep. Fish Wildl., Wash. Dep. Fish., Natl. Mar. Fish. Serv., and U.S. Fish Wildl. Serv. Avail. Bonneville Power Admin., P.O. Box 3621, Portland, OR 97208.

[2] Washington Department of Fisheries and Oregon Department of Fish and Wildlife. 1992. Status report—Columbia River fish runs and fisheries, 1938–91, 224 p. Avail. Wash. Dep. Fish., P.O. Box 999, Battle Ground, WA 98604.

[3] Melcher, C. E., and S. D. King. 1993. The 1992 lower Columbia River and Buoy 10 recreational fisheries, 77 p. Oregon Dep. Fish Wildl., 17330 S.E. Evelyn St., Clackamas, OR 97015.

Although white sturgeon supports important fisheries in the Columbia River and other rivers within its range, little is known about the spawning characteristics and early life history of this long-lived species. Using larval collections, Stevens and Miller (1970) described the distribution of white or green, *A. medirostris,* sturgeon larvae, or both, in California's Sacramento-San Joaquin River system, and Kohlhorst (1976) described sturgeon spawning in the Sacramento River. Parsley et al. (1993) described spawning and rearing habitats of white sturgeon in the Columbia River downstream from McNary Dam; however, important specific information about spawning and early life history of white sturgeon in the Columbia River downstream from Bonneville Dam was not presented.

From 1988 through 1991, we studied spawning characteristics and early life history of white sturgeon in the lower Columbia River. Primary goals of the study were 1) to define where and when spawning occurred and 2) to assess the environmental conditions at the time of spawning. Additional goals were to determine larval distribution and habitat use by young-of-the-year (YOY) white sturgeon.

Methods

Egg and larval sampling

From 1988 through 1991, white sturgeon eggs and larvae were collected in the Columbia River downstream from Bonneville Dam. The collection period varied among years; however, in all years, it extended from at least April through early July. Generally, samples were taken weekly during this period. A D-shaped plankton net was used to collect white sturgeon eggs and larvae. This net was 0.8 m wide at the bottom of the mouth opening, 0.5 m high, and constructed of 7.9-mesh/cm nylon marquisette netting. Depending on water velocity, two to six lead weights (4.5 or 9.1 kg each) were attached to the net frame to hold the net on the river bottom. A digital flow meter (General Oceanics Model 2030) was suspended in the mouth of the net to estimate the volume of water sampled. Typically, two plankton nets were fished simultaneously for about 30 minutes from an anchored 12.2-m research vessel. When water velocities at 0.2 of the total depth were greater than 2 m/s and other adverse sampling conditions were present, only one plankton net was fished, often for one hour.

Artificial substrates constructed of latex-coated animal hair also were used to collect white sturgeon eggs (McCabe and Beckman, 1990). Each artificial substrate, which was 76 × 91 cm, was enclosed in an angle-iron frame. The substrate and frame were held in place on the bottom with a three-fluke anchor similar to a grapnel. A buoy line was attached to the anchor to allow retrieval of the substrate, frame, and anchor. Artificial substrates were generally retrieved and examined weekly for eggs.

In 1990 and 1991, a 3.0-m beam trawl was used weekly or biweekly in late June, July, and August to collect white sturgeon larvae and YOY. The estimated fishing width of the trawl was 2.7 m and the height was 0.5 m. A 1.59-mm knotless nylon liner was inserted into the body of the net. The beam trawl was towed slowly upstream along the bottom for periods ranging from 2 to 20 minutes.

White sturgeon eggs and larvae were initially preserved in an approximately 4% buffered formaldehyde solution. After the eggs and larvae were processed in the laboratory, they were transferred to a 20% methanol solution. Processing of the eggs and larvae was done within 60 days after collection.

White sturgeon egg or larval sampling was conducted at various sites in the lower Columbia River from rkm 29 to 234 (Table 1, Fig. 1). Following exploratory research conducted in 1987, we decided to concentrate egg and larval sampling with stationary gear (plankton nets and artificial substrates) between rkm 172 and 234. We selected a site at rkm 230, used in previous research for monitoring white sturgeon spawning, for the most frequent egg sampling. We call this the index site.

In 1988, a 12-hour collection with a plankton net was made at the index site to determine whether catches of white sturgeon eggs and larvae changed during different light conditions. The study began at 1843 hours on 25 May and ended at 0623 hours on 26 May. Normally, one plankton net was fished for one hour during each sampling effort; 11 sampling efforts were made.

Young-of-the-year sampling

A 7.9-m (headrope length) semiballoon shrimp trawl was used to collect juvenile white sturgeon, including YOY, from 1988 through 1991. Mesh size in the trawl was 38 mm (stretched) in the body; a 10-mm mesh liner was inserted in the cod end. Trawling efforts with the shrimp trawl were normally five minutes in duration in an upstream direction, beginning when the trawl and the proper amount of cable were deployed, and ending five minutes later. Trawl speed over the bottom was usually 3 to 5 km/hour. In 1990 and 1991, a 3.0-m beam trawl was also used to collect YOY white sturgeon (see Egg and Larval Sampling section). Using a radar range-finder, we estimated the distance fished during each sampling effort. Beam trawl speed over the bottom was usually 1 to 3 km/hour.

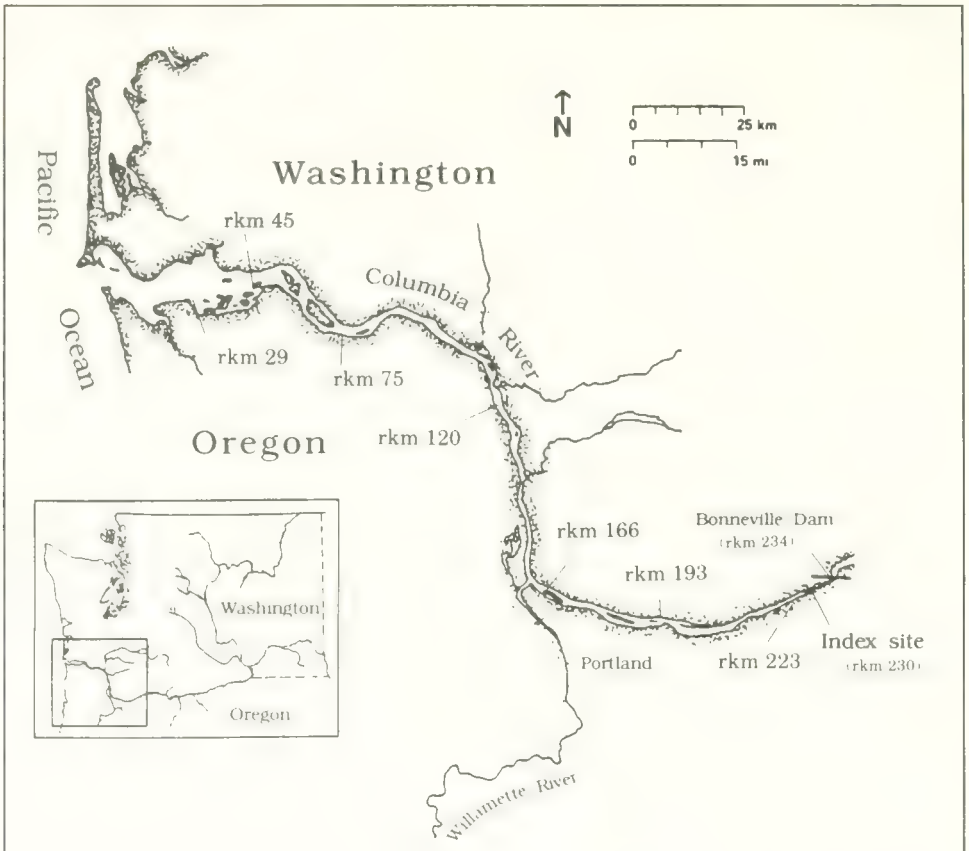

Figure 1

Location of the white sturgeon, *Acipenser transmontanus*, study area in the lower Columbia River, 1988–91.

Trawling was conducted from late March or early April through September or October of each year. In 1989, a limited amount of sampling was conducted in early November. Sampling stations were selected to determine the range of habitat used by juvenile white sturgeon and extended from rkm 29 to 218 (Table 1). Trawling effort and geographic range of sampling varied among years owing to limited personnel and gear (Table 1). In 1988 and 1989, more trawling effort was concentrated in the river upstream from rkm 120. However, in 1990 and 1991, much more trawling was done in the river between rkm 45 and 120 than in previous years. White sturgeon captured in bottom trawls were measured (total length) and weighed (g).

On 31 July and 1 August 1990, 14 trawling efforts (7.9-m shrimp trawl) were undertaken from 1155 through 0800 hours at rkm 75 to determine whether catches of juvenile white sturgeon, particularly YOY, increased during hours of darkness.

Physical conditions

Selected physical parameters were measured in conjunction with biological sampling: minimum and maximum bottom depth (m); bottom water temperature (°C); bottom water turbidity (ntu); and water velocities at 0.2 of the total depth, 0.8 of the total depth, and about 0.6 m above the bottom. By averaging water velocities measured at 0.2 and 0.8 of the total depth, we calculated a mean water column velocity (Buchanan and Somers, 1969). Water velocities were measured only during egg and larval sampling. Depth was measured with electronic depth sounders, and velocity with a Gurley current meter attached to a 45.4-kg lead fish. A Van-Dorn water bottle was used to collect water samples just above the bottom. The water temperature of each sample was measured immediately after collection, and a subsample of water was removed and placed in a glass bottle. The turbidity of the subsample was determined in the laboratory with a Hach Model 2100A Turbidimeter.

Substrate type was determined from bottom samples collected with a 0.1-m^2 Van Veen grab sampler. In addition, a substrate sample was collected at rkm 230 (index site) by scuba divers. Particle size was defined following the classifications presented in Parsley et al. (1993).

Table 1

Numbers of sampling efforts for white sturgeon, *Acipenser transmontanus*, eggs, larvae, and young of the year in the lower Columbia River, 1988–91. When two plankton nets were fished simultaneously, the data were combined and considered as one sampling effort. Location is shown in river kilometers (rkm).

Year and location	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Total
Plankton net									
1988									
rkm 172–228	0	0	8	17	1	0	0	0	26
rkm 229–230	1	2	16	5	2	1	0	0	27
rkm 231–233	1	3	6	1	0	0	0	0	11
1989									
rkm 153–171	0	0	2	0	0	0	0	0	2
rkm 172–228	0	0	18	16	5	0	0	0	39
rkm 229–230	1	2	4	5	3	1	0	0	16
rkm 231–233	0	0	1	0	0	0	0	0	1
1990									
rkm 112–171	0	0	0	1	0	0	0	0	1
rkm 172–228	0	0	29	10	3	0	0	0	42
rkm 229–230	0	5	5	4	3	0	0	0	17
rkm 231–233	0	1	2	2	0	0	0	0	5
1991									
rkm 193–228	0	1	13	8	5	0	0	0	27
rkm 229–230	0	4	4	7	6	0	0	0	21
rkm 231–233	0	0	0	0	0	0	0	0	0
Artificial substrate									
1988									
rkm 197–228	0	0	3	1	0	0	0	0	4
rkm 229–230	0	0	5	1	2	0	0	0	8
rkm 231–234	0	0	5	6	0	0	0	0	11
1989									
rkm 220–228	0	0	2	3	0	0	0	0	5
rkm 229–230	0	1	0	0	0	0	0	0	1
rkm 231–234	0	0	12	6	0	0	0	0	18
1990									
rkm 229–230	0	3	5	0	0	0	0	0	8
rkm 231–234	0	0	9	4	2	0	0	0	15
1991									
rkm 229–230	0	2	3	3	3	0	0	0	11
rkm 231–234	0	0	6	4	0	0	0	0	10
Beam trawl									
1990									
rkm 29–120	0	0	0	15	11	5	0	0	31
rkm 121–212	0	0	0	2	12	2	0	0	16
1991									
rkm 44–120	0	0	1	9	19	4	0	0	33
rkm 121–218	0	0	1	12	9	4	0	0	26
Shrimp trawl									
1988									
rkm 46–120	4	3	3	6	6	3	4	3	32
rkm 121–211	19	17	10	31	40	56	6	39	218
1989									
rkm 38–120	3	3	3	6	18	11	7	30[1]	81
rkm 121–218	17	24	34	40	50	67	25	49	306
1990									
rkm 45–120	0	42	29	24	27	37	13	32	204
rkm 121–212	0	18	21	0	19	5	4	23	90
1991									
rkm 45–120	0	33	29	16	15	30	31	0	154
rkm 121–212	0	24	2	20	21	1	25	0	93

[1] Includes eight sampling efforts conducted in November

Data analyses

The developmental stages of white sturgeon eggs were determined from descriptions by Beer (1981). Timing of spawning was estimated from developmental stages of eggs and temperature-egg developmental data from Wang et al. (1985). Water temperature at the time of egg collection was used in making the estimates, and a daily index of spawning activity was calculated from these estimated spawning dates. The index of spawning activity was treated as a dichotomous variable: spawning occurred or did not occur on a particular day.

Stepwise regression (Ryan et al., 1985) was used to determine relationships between the abundance of freshly fertilized (stage 2) white sturgeon eggs collected in plankton nets at the index site and physical parameters, including water temperature, turbidity, mean water column velocity, near-bottom water velocity, and Bonneville Dam discharge. Stage-2 eggs were assumed to be approximately three hours old or less (Beer, 1981). Bonneville Dam discharge for these comparisons was estimated by averaging hourly discharge at the time of sampling with discharges during the three hours prior to sampling. White sturgeon egg abundance and all physical parameters were tested for normality. Egg abundance (eggs/1,000 m^3) and turbidity failed the test for normality; both were normalized by using a $\log_{10}$ transformation. Data collected just prior to, during, and just after the spawning period were used for the regression analyses. Transformed egg abundance was also plotted against each of the above physical parameters to investigate the possibility of nonlinear relationships. The plots suggested that the relationship between egg abundance and water temperature may be nonlinear; therefore, we used second-degree polynomial (quadratic) regression (Ryan et al., 1985) to examine this relationship.

For data analysis, YOY white sturgeon were separated from older juvenile sturgeon by length. A YOY was defined as being between 25 and 325 mm total length and less than one year old. Sturgeon shorter than 25 mm were considered larvae. A white sturgeon's birth date was assumed to be 1 January, although in reality the birth date was generally later in the year.

Results

Eggs

The number of white sturgeon eggs collected from 1988 through 1991 ranged from 1,404 in 1988 to 2,785 in 1990 (Table 2); however, sampling effort was not equal each year. The percent of white sturgeon eggs collected in plankton nets, as opposed to artificial substrates, also varied annually, ranging from 37% in 1991 to 87% in 1989. Virtually all white sturgeon eggs were collected in the 11-km section of river extending from rkm 223 to 234, immediately downstream from Bonneville Dam. In both 1990 and 1991, four white sturgeon eggs were collected at rkm 193. In all years, 4% or less of white sturgeon eggs collected in plankton nets were infected with fungus, indicating infertile or dead eggs.

From the spawning index, which was derived from back calculations by using the developmental stages of all eggs, we estimated that spawning occurred on 38 days in 1988, from 22 April to 22 June, and that 58% of the spawning days were in May (Fig. 2). In 1989, spawning occurred on an estimated 43 days, from 22 April to 2 July, and 53% of the spawning days were in May. In 1990, spawning was estimated to have occurred on at least 48 days, from 23 April to 14 July, and 46% of the spawning days were in May. Finally, for 1991, we estimated that spawning occurred on 39 days, from 5 May to 14 July, and 56% of the spawning days were in May.

Water temperatures measured at Bonneville Dam and at sampling sites during the spawning period varied annually (Fig. 2). Water temperatures at Bonneville Dam sometimes differed by about 1°C from those at egg collection sites. From 1988 to 1991, white sturgeon spawned at water temperatures ranging from 10 to 19°C (Bonneville Dam or sampling site temperatures).

Bonneville Dam discharge (mean hourly discharge by day) also varied annually (Fig. 2). The highest daily flows through Bonneville Dam during the sampling periods occurred during the spawning periods in 1990 and 1991. Combining data from all years, we concluded that spawning occurred on days with mean discharges ranging from 3,399 to 10,505 m^3/s.

During the 4-year study, stage-2 eggs were collected at temperatures from 10 to 18°C, turbidities from 2.2 to 11.5 ntu, near-bottom velocities from 0.6 to 2.4 m/s, mean water column velocities from 1.0 to 2.8 m/s, and depths from 3 to 23 m.

White sturgeon spawned primarily in the area upstream from rkm 222. Virtually all stage-2 eggs were collected between rkm 223 and rkm 234 (about 600 m downstream from the spillways at Bonneville Dam). Small numbers of stage-2 eggs were collected at rkm 193—three in 1990 and one in 1991. Exact spawning locations could not be determined because it was not possible to measure the distance that white sturgeon eggs were carried by the river current immediately after spawning. In addition, at least some white sturgeon eggs, which adhere to bottom sub-

strate, were dislodged by water currents and carried downstream.

Substrate in the river section, where stage-2 eggs were most abundant, was primarily cobble and boulder. We are not sure of the composition of the substrate near rkm 193; however, there are small rocky islands in the area, and on occasion large amounts of sand were collected in the plankton net. In addition, there is a rocky reef several kilometers upstream from this sampling site.

At the index site, stage-2 eggs were collected over a range of environmental conditions from 1988 through 1991 (Table 3). Water temperatures ranged from 10 to 18°C, bottom water turbidities from 2.2 to

Table 2

Numbers of white sturgeon, *Acipenser transmontanus*, eggs and larvae collected in the Columbia River downstream from Bonneville Dam, 1988–91. Plankton nets and artificial substrates were used to collect eggs; plankton nets and a 3.0-m beam trawl (in 1990 and 1991) were used to collect larvae. Area refers to the geographic range (in river kilometers [rkm]) over which eggs or larvae were collected. Fungus-infected eggs collected in plankton nets are shown in parentheses and are included in the numbers reported for the nets. A dash (—) indicates that no sampling was conducted.

	Eggs			Larvae		
Sampling period	Area (rkm)	Net	Substrate	Area (rkm)	Net	Trawl
1988						
15–30 Apr	230–231	19	—		0	—
1–15 May	228–233	163 (1)	46	228–230	11	—
16–31 May	230–233	405 (10)	539	193–231	71	—
1–15 Jun	226–234	112 (5)	84	181–230	5	—
16–30 Jun	226–230	20 (1)	16	226	3	—
1–15 Jul		0	0		0	—
16–31 Jul		0	0		0	—
Total		719 (17)	685		90	—
1989						
15–30 Apr	230	385	47		0	—
1–15 May	224–234	275 (1)	37	174–232	19	—
16–31 May	224–234	703 (6)	212	181–230	39	—
1–15 Jun	222–234	640 (23)	9	193–230	64	
16–30 Jun	226–230	13 (3)	0	181–230	13	—
1–15 Jul	226	2 (1)	—		0	—
16–31 Jul		0	—		0	—
Total		2,018 (34)	305		135	
1990						
15–30 Apr	230–231	386	258		0	—
1–15 May	223–234	904 (38)	153	223–232	34	—
16–31 May	193–234	187 (7)	275	181–230	34	—
1–15 Jun	224–234	210 (8)	260	112–230	33	—
16–30 Jun	224–230	109 (20)	0	45–230	41	12
1–15 Jul	226–234	8	35	67–226	1	25
16–31 Jul		0	0	127–230	9	1
Total		1,804 (73)	981		152	38
1991						
15–30 Apr		0	0		0	—
1–15 May	224–234	129 (1)	589		0	—
16–31 May	193–234	303 (3)	265	193–230	28	0
1–15 Jun	226–234	46 (7)	205	193–230	17	
16–30 Jun	224–234	227 (1)	164	45–230	45	33
1–15 Jul	193–230	30 (2)	50	98–230	37	18
16–31 Jul		0	0		0	0
Total		735 (14)	1,273		127	51

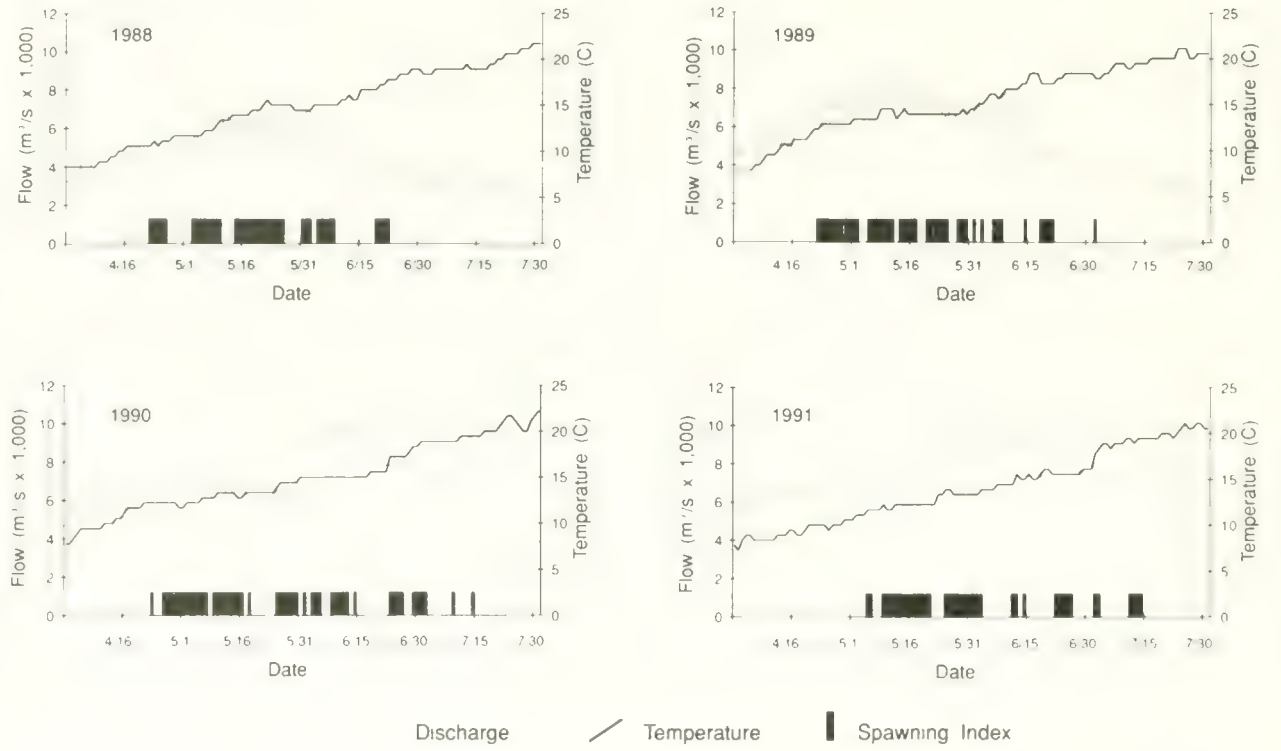

Figure 2

Water temperatures (°C) and Bonneville Dam discharges (mean hourly water discharges by day) from 1 April through 31 July (1988–91); discharge is shown as $m^3/s \times 1{,}000$. Water temperatures were measured at Bonneville Dam. The spawning index shows the days on which we estimated that white sturgeon spawned.

11.5 ntu, near-bottom water velocities from 1.0 to 2.1 m/s, and mean water column velocities from 1.5 to 2.6 m/s. Estimated Bonneville Dam discharges at the index site during spawning ranged from 3,890 to 9,600 m^3/s. In all years, the highest egg catches occurred during late April or May.

Results from stepwise regression indicated that water temperature and mean water column velocity together were the best predictors of stage-2 egg collections at the index site; however, they explained only 27.1% of the variation in the egg collections. The regression equation was $\log_{10}$ (number of eggs plus one/1,000 m^3) = 1.01 – 0.110 (water temperature) + 0.637 (mean water column velocity); F = 7.99 and P = 0.001. Bottom water turbidity was an important predictor in the first three steps of the stepwise regression, but dropped out in the fourth and final step. If a high turbidity value and accompanying zero egg catch (18 April 1989; see Table 3) are removed from the stepwise regression, the results change. Excluding the turbidity data for 18 April 1989, stepwise regression indicated that water temperature and turbidity together were the best predictors of stage-2 egg collections at the index site. The regression equation was $\log_{10}$ (number of eggs plus one/1,000 m^3) = 0.937 – 0.0857 (water temperature) + 1.70 ($\log_{10}$ turbidity); F=11.65, P=0.000, and r^2=35.7%. Second-degree polynomial regression indicated a significant relationship between stage-2 egg collections and water temperature (F=8.70, P=0.001, and r^2=28.8%). The regression equation was $\log_{10}$ (number of eggs plus one/1,000 m^3) = –4.44 + 0.846 (water temperature) – 0.0326 (water temperature^2).

Catches of freshly fertilized white sturgeon eggs during the 12-hour collection at the index site fluctuated; catches ranged from 0.0 to 72.2 eggs/1,000 m^3 (Table 4). On the basis of collections of freshly fertilized eggs during the 12-hour collection and daylight collections during the 4 years, it appears that adult white sturgeon spawn throughout the 24-hour day.

Larvae

White sturgeon larvae were collected from rkm 45 to rkm 232 in the lower Columbia River from 1988 through 1991 (Table 2), suggesting wide dispersal

Table 3

White sturgeon, *Acipenser transmontanus*, egg (freshly fertilized) catches and accompanying physical measurements for the index site near rkm 230 in the lower Columbia River, 1988–91. Water temperatures (on site), turbidities, and bottom velocities were measured just above the bottom; Bonneville Dam flow was the average of the hourly discharges at the time of sampling and during the three hours prior to sampling.

Date	Temperature (°C)	Turbidity (ntu)	Velocity (m/s)		Dam flow ($m^3/s \times 1{,}000$)	No. eggs	Eggs/ 1,000 m^3
			Bottom	Mean column			
1988							
25 Apr	10	4.5	1.0	1.5	3.89	3	1.7
5 May	11	6.4	1.4	1.8	5.14	24	19.5
10 May	13	6.0	1.0	1.6	5.95	80	54.1
18 May	13	6.0	1.2	1.6	6.24	4	2.1
23 May	14	5.4	1.2	2.1	5.59	10	6.4
2 Jun	14	6.0	1.4	2.3	6.51	18	10.3
8 Jun	14	3.5	1.4	2.0	5.43	19	12.4
16 Jun	16	3.5	1.1	1.8	4.50	0	0.0
20 Jun	16	3.2	1.1	1.5	4.17	9	6.9
29 Jun	17	3.1	1.0	1.6	3.90	0	0.0
1989							
18 Apr	10	12.0	1.5	1.9	6.46	0	0.0
27 Apr	12	10.0	1.5	2.2	7.11	348	219.9
1 May	12	7.5	1.7	2.0	6.96	17	10.3
10 May	13	7.5	—	2.4	7.89	70	40.9
17 May	14	9.2	1.6	2.3	8.30	525	284.5
24 May	14	5.9	1.4	2.2	6.82	18	10.8
1 Jun	14	5.4	1.6	2.2	6.80	1	0.6
8 Jun	16	5.3	2.0	2.6	7.66	99	58.3
15 Jun	17	3.4	1.5	2.2	5.91	0	0.0
21 Jun	17	3.7	1.0	1.9	4.60	0	0.0
28 Jun	18	3.3	1.1	1.6	3.98	0	0.0
6 Jul	19	3.5	1.0	1.6	3.72	0	0.0
1990							
23 Apr	11	3.0	1.1	1.5	6.61	0	0.0
30 Apr	11	3.5	1.1	2.2	7.20	225	133.2
7 May	12	3.9	1.7	2.6	7.57	32	14.8
14 May	12	3.7	1.8	2.3	7.03	292	166.9
22 May	13	3.0	1.1	1.7	4.69	0	0.0
29 May	14	3.0	1.4	2.3	5.90	39	25.6
5 Jun	15	3.4	1.7	2.5	8.32	19	10.0
11 Jun	15	6.5	1.5	2.4	9.07	23	12.9
18 Jun	15	5.6	2.1	2.7	9.01	0	0.0
25 Jun	17	3.7	1.7	2.5	7.52	2	1.1
2 Jul	18	2.2	1.2	2.1	6.71	1	0.5
9 Jul	19	1.9	1.1	2.2	5.56	0	0.0
18 Jul	20	2.0	1.1	1.8	4.25	0	0.0
1991							
30 Apr	10	3.6	1.3	2.1	7.67	0	0.0
6 May	11	3.0	1.3	2.1	6.80	2	1.2
14 May	12	4.2	1.4	2.0	6.81	98	56.5
20 May	12	5.3	2.1	2.6	9.60	15	14.4
29 May	14	6.3	1.5	2.6	8.79	2	1.4
3 Jun	14	11.5	2.1	2.6	9.10	11	7.1
19 Jun	16	4.2	1.4	2.5	7.39	0	0.0
26 Jun	15	3.7	1.1	2.2	7.36	12	7.5
3 Jul	18	4.3	1.7	2.4	7.38	9	5.2
9 Jul	19	2.8	1.2	1.6	5.55	0	0.0
15 Jul	19	3.5	1.0	1.8	5.40	0	0.0

Table 4

Summary of white sturgeon, *Acipenser transmontanus*, egg (freshly fertilized) and larval collections during a 12-h study at the index site near rkm 230 in the lower Columbia River. Sampling was done from 1843 hours on 25 May to 0623 hours on 26 May 1988 with a plankton net. Bonneville Dam flow was the average of hourly discharges at the time of sampling and during the 3 hours prior to sampling.

Sampling times (h)[1]	Bonneville Dam flow ($m^3/s \times 1{,}000$)	Eggs		Larvae	
		No.	No./1,000 m^3	No.	No./1,000 m^3
1843–1943	7.24	4	2.8	9	6.4
1951–2051[2]	7.40	3	2.3	0	0.0
2100–2200	7.00	0	0.0	5	3.3
2206–2306	6.74	108	72.2	7	4.7
2314–0014	6.50	7	4.7	9	6.0
0020–0120	6.51	27	18.2	9	6.1
0128–0228	6.58	34	21.9	3	1.9
0234–0334	6.66	3	2.0	7	4.7
0340–0440	6.72	1	0.7	8	5.3
0445–0545	6.77	32	20.6	1	0.6
0553–0623	6.76	18	22.6	7	8.8

[1] Sunset on 25 May was at 2030 hours; sunrise on 26 May was at 0515 hours.
[2] Questionable sampling effort; net was damaged.

after hatching. River kilometer 45 is located in the upper end of the Columbia River estuary (Fig. 1); however, this section of the estuary is a freshwater environment. Larvae were collected from early May through late July, reflecting a protracted spawning period (Table 2). All white sturgeon larvae in 1988 and 1989, and 71% or more in 1990 and 1991, were collected in plankton nets. In 1988 and 1989, larvae were not collected as far downstream as in 1990 and 1991. Undoubtedly, smaller areas of capture in 1988 and 1989 were due to lack of sampling with the 3.0-m beam trawl in these years. All white sturgeon larvae collected in the upper estuary in 1990 and 1991 were collected in the beam trawl. Larvae were collected at depths ranging from 4 to 29 m. When the larvae were collected in plankton nets, they were most likely being transported by water currents, because the nets were fished from an anchored boat.

Catches of white sturgeon larvae during the 12-hour collection at the index site fluctuated with catches ranging from 0.0 to 8.8 larvae/1,000 m^3 (Table 4).

Young of the year

Annual catches of YOY white sturgeon varied considerably, ranging from 11 in 1988 to 273 in 1990 (Table 5). Annual catches shown in Table 5 are not necessarily indicative of YOY abundance in respective years, because sampling gears and schemes were not the same each year. In 1988 and 1989, the 3.0-m beam trawl was not used, whereas in 1990 and 1991 it was used. The beam trawl was more effective at capturing small YOY white sturgeon than was the 7.9-m semiballoon shrimp trawl. Also, in 1990 and 1991, more sampling was conducted in the lower 120 km of the river than in 1988 and 1989.

On the basis of sampling from 1988 through 1991, it appears that YOY white sturgeon are primarily using the section of river extending from rkm 45 to 166 (Table 5). Relatively few YOY white sturgeon were collected in the 68 km of river between Bonneville Dam (rkm 234) and rkm 166; small catches were made at rkm 211 in July 1990 and September 1991.

In 1990 and 1991, YOY white sturgeon were first captured in late June, less than two months after spawning was estimated to have begun. In all four years, YOY white sturgeon appeared to grow well during their first summer; however, monthly mean lengths and weights varied among years (Table 5). During all years, YOY white sturgeon reached a minimum mean total length of 176 mm and a minimum mean weight of 30 g by the end of September. No statistical comparisons among years were done because of small sample sizes, the protracted spawning period of white sturgeon, and the fact that YOY white sturgeon were collected throughout the month.

The YOY white sturgeon were more abundant in deeper areas of the lower Columbia River, at least during daylight; mean minimum depths during trawling efforts in which YOY were captured were ≥12.5 m in all years. Mean maximum depths at which YOY white sturgeon were captured were ≥ 15.8 m in all years. Bottom substrate over which YOY white

Table 5

Summary of young-of-the-year white sturgeon, *Acipenser transmontanus*, catches in the Columbia River downstream from Bonneville Dam, 1988–91. SD = standard deviation.

			Total length (mm)		Weight (g)	
Month	Capture location (rkm)	Number	Mean	SD	Mean	SD
1988						
Jul	126	1	86.0	0.0	3.0	0.0
Aug	127–153	2	134.0	41.0	13.0	9.9
Sep	153	2	235.0	35.4	60.5	29.0
Oct	127–162	6	248.3	9.8	68.2	8.9
Total		11				
1989						
Jul	49–153	17	93.4	25.8	5.0	3.1
Aug	49–153	15	176.7	29.9	31.6	13.5
Sep	46–153	12	224.4	30.4	59.7	18.7
Oct	49–162	56	269.4	23.5	87.4	18.5
Nov[1]	107–120	11	273.8	17.7	90.4	20.2
Total		111				
1990[2]						
Jun	45–120	7	32.1	4.3	<1.0	<1.0
Jul	45–211	125	75.6	27.3	3.2	2.8
Aug	50–166	79	123.8	37.5	12.3	10.4
Sep	49–166	14	222.6	28.4	54.4	19.8
Oct	46–166	48	224.4	28.5	51.9	17.4
Total		273				
1991[3]						
Jun	45–166	27	30.4	4.1	<1.0	<1.0
Jul	45–166	89	55.7	17.8	1.3	1.2
Aug	49–127	55	97.1	27.6	6.1	4.8
Sep	45–211	47	176.4	38.3	29.8	16.2
Total		218				

[1] Sampling for November was conducted on 1 November 1989.
[2] Includes samples collected at rkm 75 from 31 July to 1 August 1990.
[3] No sampling was done in October 1991.

sturgeon were found was predominantly sand; however, much of the bottom in the lower Columbia River is composed of sand. In addition, the bottom trawls could not be used in rocky areas.

During the 20-hour sampling survey from 31 July to 1 August 1990 (sampled from 1155 through 0800 hours) at rkm 75, 52 YOY white sturgeon were collected (Table 6). Over 78% of YOY white sturgeon were collected during hours of darkness, indicating that they were more vulnerable to the trawl at night or that they moved into the sampling area at night. The YOY were collected at depths that ranged from 11 to 15 m.

Discussion

White sturgeon successfully spawned in the lower Columbia River in all years of the study. All white sturgeon eggs collected downstream from Bonneville Dam were probably released by sturgeon spawning in this area and not by sturgeon spawning in the impoundment created by Bonneville Dam. Although white sturgeon spawn in the impoundment upstream from Bonneville Dam (Miller et al.[4]), it is unlikely that any of these eggs are carried through Bonneville Dam. In 1990, Miller et al.[4] collected white sturgeon eggs between rkm 298 and 308. The locations of white sturgeon egg collections upstream from Bonneville

[4] Miller, A. I., P. J. Anders, M. J. Parsley, C. R. Spraque, J. J. Warren, and L. G. Beckman. 1991. Report C. *In* A. A. Nigro (ed.), Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, p. 82–144. Ann. Rep. to Bonneville Power Admin. (Project 86-50) by Oreg. Dep. Fish Wildl., Wash. Dep. Fish., Natl. Mar. Fish. Serv., and U.S. Fish Wildl. Serv. Avail. Bonneville Power Admin., P.O. Box 3621, Portland, OR 97208.

Dam strongly suggest that eggs are found only in the upper Bonneville Pool, since rkm 298 is about 64 km upstream from the dam.

Spawning in the lower Columbia River in 1988–91 occurred during temperature regimes for successful egg incubation. Successful egg incubation for white sturgeon occurs at temperatures between 10 and 18°C; highest survival and uniform hatching occur between 14 and 16°C (Wang et al., 1985). In our study, we estimated that peak spawning occurred at water temperatures of 12 to 14°C. We estimated that some spawning occurred at water temperatures of 18 or 19°C. Survival for these eggs was probably less than for eggs spawned at lower water temperatures. Wang et al. (1985) observed that substantial white sturgeon embryo mortalities may occur at water temperatures of 18 to 20°C and that temperatures greater than 20°C are clearly lethal. In the Sacramento River, Kohlhorst (1976) observed that water temperatures during the white and green sturgeon spawning period ranged from 7.8 to 17.8°C and that peak spawning occurred at about 14.4°C. It should be noted that Kohlhorst's estimates of the spawning period are based on back calculations of larval ages, rather than on sturgeon eggs. Spawning dates can be more accurately estimated by using eggs rather than larvae.

Sampling for white sturgeon larvae was done with gear that sampled along or very near the bottom; therefore, no data were collected regarding vertical distribution of white sturgeon larvae. However, Stevens and Miller (1970) reported that white or green sturgeon larvae, or both, are primarily demersal in the Sacramento-San Joaquin River System. They caught 33 larvae in 16 bottom sampling efforts and only one larva in eight surface and midwater efforts.

River currents disperse white sturgeon larvae out of spawning and egg incubation areas. Stevens and Miller (1970) noted a direct relationship between river flow and catches of white or green sturgeon larvae, or both, in the Sacramento-San Joaquin Delta. In a laboratory experiment, Brannon et al.[5] observed that white sturgeon larvae swam up the water column after hatching. In addition, Brannon et al.[5] found that the behavior of white sturgeon larvae was affected by current velocity in laboratory experiments. There was an inverse relationship between water velocity and the amount of time larvae spent in the water column.

Dispersal of white sturgeon larvae over a wide area is probably very important in maintaining a stable population of white sturgeon in the lower Columbia River. Wide dispersal allows utilization of more feeding areas and rearing habitats by larval and postlarval white sturgeon and minimizes competition for these limited resources. However, it is also important that white sturgeon not be carried into saline portions of the Columbia River estuary. Brannon et al.[5] found that salinities ≥16 ppt killed white sturgeon larvae and fry.

Food resources for YOY white sturgeon in many of the deeper areas (>12 m) of the lower Columbia River are probably not abundant. Little is known about the diet of YOY white sturgeon in the lower Columbia River; however, limited observations suggest that the amphipod *Corophium salmonis* is the primary prey (Muir et al., 1988). Densities of *C. salmonis* in many of the deeper areas probably are low because of unstable substrates. *Corophium salmonis* is a tube-builder and requires a more stable substrate to densely populate an area. In 1990, densities of *C. salmonis* at a deep area (19–21 m) at rkm 153 aver-

[5] Brannon, E., S. Brewer, A. Setter, M. Miller, F. Utter, and W. Hershberger. 1985. Columbia River white sturgeon (*Acipenser transmontanus*) early life history and genetics study. Final Rep. to Bonneville Power Admin. (Project 83–316) by Univ. Wash. and Natl. Mar. Fish. Serv., Seattle, 68 p. Avail. Bonneville Power Admin., P.O. Box 3621, Portland, OR 97208.

Table 6

Summary of young-of-the-year white sturgeon, *Acipenser transmontanus*, catches during a 20-hour study at rkm 75 in the lower Columbia River, 31 July–1 August 1990. Sampling was done from 1155 hours on 31 July to 0800 hours on 1 August with a 7.9-m semiballoon shrimp trawl.

Hour[1]	Depth range	No.	No./ha	Length range (mm)	Hour[1]	Depth range	No.	No./ha	Length range (mm)
1155	13–14 m	0	0	—	2130	12–14 m	12	39	57–120
1357	13–14 m	0	0	—	2230	13–15 m	12	38	54–122
1533	10–15 m	0	0	—	0030	12–14 m	15	55	61–141
1702	13–14 m	1	4	79	0218	12–14 m	2	10	82–86
1830	12–14 m	1	4	108	0527	13 m	0	0	—
1933	11–14 m	6	21	79–114	0646	12–13 m	2	10	86–113
2029	12–14 m	1	4	79	0800	12–13 m	0	0	—

[1] Sunset on 31 July was at 2047 hours; sunrise on 1 August was at 0555 hours.

aged less than 105 organisms/m^2 in June through September (McCabe and Hinton[6]). However, in a deep area at rkm 120 that had large numbers of YOY white sturgeon, the density of *C. salmonis* was relatively high in August 1990 (2,289/m^2) but dropped to 433 organisms/m^2 in September (McCabe and Hinton[6]). More research is needed to assess the abundance of benthic organisms in rearing areas of YOY white sturgeon.

Although prey abundance may be low in many of the deeper areas of the lower Columbia River, the substrate in these areas is probably ideal for efficient feeding by YOY white sturgeon. The white sturgeon has a protrusible mouth that is used to suck prey from the bottom. In a laboratory experiment with juvenile Russian sturgeon, *Acipenser gueldenstaedti*, Sbikin and Bibikov (1988) observed that juveniles (≤130 mm) preferred even, sandy bottoms to bottoms with stones or depressions. Juveniles avoided vegetated areas.

Apparently YOY white sturgeon are very effective and efficient predators on prey found in the rearing areas, as evidenced by their rapid growth during the summer and early fall. The YOY white sturgeon reached a mean total length of at least 176 mm by the end of September. Rapid growth during the first growing season reduces natural mortality; by the end of summer or fall, YOY white sturgeon in the lower Columbia River probably have few natural predators.

Sampling equipment used to collect YOY white sturgeon in the lower Columbia River was limited to two types of bottom trawls that could not be used in shallow littoral areas. Observations made during other studies suggest that YOY white sturgeon do not use shallow littoral areas. No YOY white sturgeon have been collected in intensive beach seining efforts at rkm 75 during the last 15 years.[7] Most sampling was done during daylight; limited sampling was done at night. The beach seining location was adjacent to the sampling site where 52 YOY white sturgeon were collected during a 20-hour study in 1990. No YOY white sturgeon were collected in backwaters and shoreline areas during limited beach seining tows in the lower Columbia River in August 1988 (McCabe et al.[8]).

We conclude that white sturgeon spawned successfully in the lower Columbia River during the period 1988 through 1991. Collection of YOY white sturgeon indicated that recruitment occurred in all years.

[6] McCabe, G. T., Jr., and S. A. Hinton. 1991. Report D. *In* A. A. Nigro (ed.), Status and habitat requirements of white sturgeon populations in the Columbia River downstream from McNary Dam, p. 145–180. Ann. Rep. to Bonneville Power Admin. (Project 86–50) by Oreg. Dep. Fish Wildl., Wash. Dep. Fish., Natl. Mar. Fish. Serv., and U.S. Fish Wildl. Serv. Avail. Bonneville Power Admin., P.O. Box 3621, Portland, OR 97208.

[7] Richard D. Ledgerwood, National Marine Fisheries Service, P.O. Box 155, Hammond, Oregon 97121. Personal commun., 1992.

[8] McCabe, G. T., Jr., S. A. Hinton, and R. J. McConnell. 1989. Report D. *In* A. A. Nigro (ed.), Status and habitat requirements of white sturgeon populations in the Columbia River downstream from McNary Dam, p. 167–207. Ann. Rep. to Bonneville Power Admin. (Project 86–50) by Oreg. Dep. Fish Wildl., Wash. Dep. Fish., Natl. Mar. Fish. Serv., and U.S. Fish Wildl. Serv. Avail. Bonneville Power Admin., P.O. Box 3621, Portland, OR 97208.

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Literature cited

Beer, K. E.
1981. Embryonic and larval development of white sturgeon (*Acipenser transmontanus*). M.S. thesis, Univ. Calif., Davis, 93 p.

Buchanan, T. J., and W. P. Somers.
1969. Discharge measurements at gaging stations, Chapter A8, 65 p. Techniques of water-resources investigations of the United States Geological Survey, Book 3, Applications of hydraulics. U.S. Gov. Printing Office, Washington, D.C.

Cochnauer, T. G., J. R. Lukens, and F. E. Partridge.
1985. Status of white sturgeon, *Acipenser transmontanus*, in Idaho. *In* F. P. Binkowski and S. I. Doroshov (eds.), North American sturgeons: biology and aquaculture potential, p. 127–133. Dr. W. Junk, Dordrecht, Netherlands.

Craig, J. A., and R. L. Hacker.
1940. The history and development of the fisheries of the Columbia River. U.S. Dep. Interior, Bur. Fish., Bull. 32(49):133–216.

Kohlhorst, D. W.
1976. Sturgeon spawning in the Sacramento River in 1973, as determined by distribution of larvae. Calif. Fish Game 62:32–40.

McCabe, G. T., Jr., and L. G. Beckman.
1990. Use of an artificial substrate to collect white sturgeon eggs. Calif. Fish Game 76:248–250.

Muir, W. D., R. L. Emmett, and R. J. McConnell.
1988. Diet of juvenile and subadult white sturgeon in the lower Columbia River and its estuary. Calif. Fish Game 74:49–54.

Parsley, M. J., L. G. Beckman, and G. T. McCabe Jr.
1993. Spawning and rearing habitat use by white sturgeons in the Columbia River downstream from McNary Dam. Trans. Am. Fish. Soc. 122:217–227.

Ryan, B. F., B. L. Joiner, and T. A. Ryan Jr.
1985. Minitab handbook. PWS-KENT Pub. Co., Boston, MA, 386 p.

Sbikin, Yu. N., and N. I. Bibikov.
1988. The reaction of juvenile sturgeons to elements of bottom topography. J. Ichthyol. 28:155–160.

Scott, W. B., and E. J. Crossman.
1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184, 966 p.

Stevens, D. E., and L. W. Miller.
1970. Distribution of sturgeon larvae in the Sacramento-San Joaquin River system. Calif. Fish Game 56:80–86.

Wang, Y. L., F. P. Binkowski, and S. I. Doroshov.
1985. Effect of temperature on early development of white and lake sturgeon, *Acipenser transmontanus* and *A. fulvescens*. Environ. Biol. Fishes 14:43–50.

Cetaceans on the upper continental slope in the north-central Gulf of Mexico

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Abstract.—Little is known about cetaceans in the oceanic Gulf of Mexico (depths >200 m). From July 1989 to June 1990, we conducted aerial surveys in the oceanic north-central Gulf (long. 87.5°W–90.5°W) with the following objectives: 1) to determine which cetacean species were present; 2) to document temporal and spatial distribution for each species; and 3) to estimate relative abundance for each species. We surveyed a total of 20,593 transect km and sighted at least 18 species. Of 278 identified herds (6,084 animals), 94% of the herds and 98% of the animals represented seven species or species groups: Risso's dolphin, *Grampus griseus* (22% of the herds, 13% of the animals); sperm whale, *Physeter macrocephalus* (16%, 1%); bottlenose dolphin, *Tursiops truncatus* 14%, 7%); Atlantic spotted dolphin, *Stenella frontalis* (13%, 15%); pygmy sperm whale, *Kogia breviceps*, and dwarf sperm whale, *Kogia simus* (12%, 1%); striped dolphin, *Stenella coeruleoalba*, spinner dolphin, *S. longirostris*, and clymene dolphin, *S. clymene* (9%, 34%); and pantropical spotted dolphin, *S. attenuata* (8%, 27%). Each of these species or species groups was sighted throughout the area surveyed in at least three seasons. Mean water depths of bottlenose dolphin and Atlantic spotted dolphin sightings were less than 400 m; mean water depths of Risso's dolphins and pygmy and dwarf sperm whales were between 400-600 m; and mean water depths of striped, spinner, and clymene dolphins, sperm whales, and pantropical spotted dolphins were greater than 700 m. Mean herd sizes varied by species and species groups and ranged from 1.9 animals for pygmy and dwarf sperm whales to 87.8 animals for striped, spinner, and clymene dolphins.

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The Gulf of Mexico encompasses an area of over 1,500,000 km^2 and has an average depth of 1,700 m (Gore, 1992). The continental shelf (depths <200 m) is wide (up to 260 km) in most parts of the northern Gulf (Fig. 1). Directed studies (Fritts et al., 1983; Scott et al.[1]) and opportunistic sightings (Schmidly, 1981; Rademacher[2]) have suggested that only the bottlenose dolphin, *Tursiops truncatus*, and the Atlantic spotted dolphin, *Stenella frontalis*, are common in most continental shelf waters of the U.S. Gulf. However, there are records (primarily from strandings) of 29 cetacean species from the Gulf (Schmidly, 1981; Perrin et al., 1981; Hersh and Odell, 1986; Perrin et al., 1987; Bonde and O'Shea, 1989; Barron and Jefferson, 1993). Therefore, if species other than the bottlenose dolphin and the Atlantic spotted dolphin are represented in substantial numbers, their distributions must be primarily oceanic (depths >200 m).

Mineral deposits have been mined widely in U.S. Gulf shelf waters west of Mobile, Alabama, and as of 1988, over 4,500 drilling structures have been in use for oil and gas production. Mineral development on the continental slope (depths 200–2,000 m) in the central and western Gulf has begun and additional exploratory drilling is being planned. Before large-scale exploration, development, and production can take place, an assessment of cetacean diversity, distribution, and abundance is required to satisfy the intent of the U.S. Marine Mammal Protection Act and the U.S. Endangered Species Act. Both acts mandate that federal agencies take appropriate actions to ensure that their activities do not

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[1] Scott, G. P., D. M. Burn, L. J. Hansen, and R. E. Owen. 1989. Estimates of bottlenose dolphin abundance in the Gulf of Mexico from regional aerial surveys. U.S. Dep. Commer., NOAA, Nat. Mar. Fish. Serv., Southeast Fish. Sci. Cent., Miami Laboratory, 75 Virginia Beach Drive, Miami, FL 33149. Admin. Rep. CRD-88/89-07, 24 p.

[2] Rademacher, K. R. 1991. Opportunistic sightings of cetaceans in the Gulf of Mexico from NOAA Ship *Chapman*, 1989–90. U.S. Dep. Commer., NOAA, Nat. Mar. Fish. Serv., Southeast Fish. Sci. Cent., Pascagoula Facility, P.O. Drawer 1207, Pascagoula, MS 39568. Unpubl. data.

contribute to the demise of endangered species or to the depletion of marine mammal populations. To assess potential impacts of oil and gas activities on marine mammal populations, it is imperative that we know when, where, and how many marine mammals may be vulnerable to such activities.

Only limited data from strandings, opportunistic sightings (Schmidly, 1981; Mead[3]), and aerial surveys (Fritts et al., 1983) are currently available to assess these parameters for oceanic cetaceans in the Gulf. In July 1989, the U.S. Minerals Management Service and the Southeast Fisheries Science Center (SEFSC) began aerial surveys of cetaceans on the upper continental slope in the north-central Gulf. The objectives of the surveys were 1) to determine which species were present; 2) to document temporal and spatial distribution for each species; and 3) to estimate relative abundance for each species.

[3] Mead, J. G. 1992. Marine mammal strandings. National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Unpubl. data.

Methods

The study was conducted in two phases. Phase 1 was a five-month pilot study carried out from July through November 1989. The primary objective of Phase 1 was to determine which species of cetaceans,

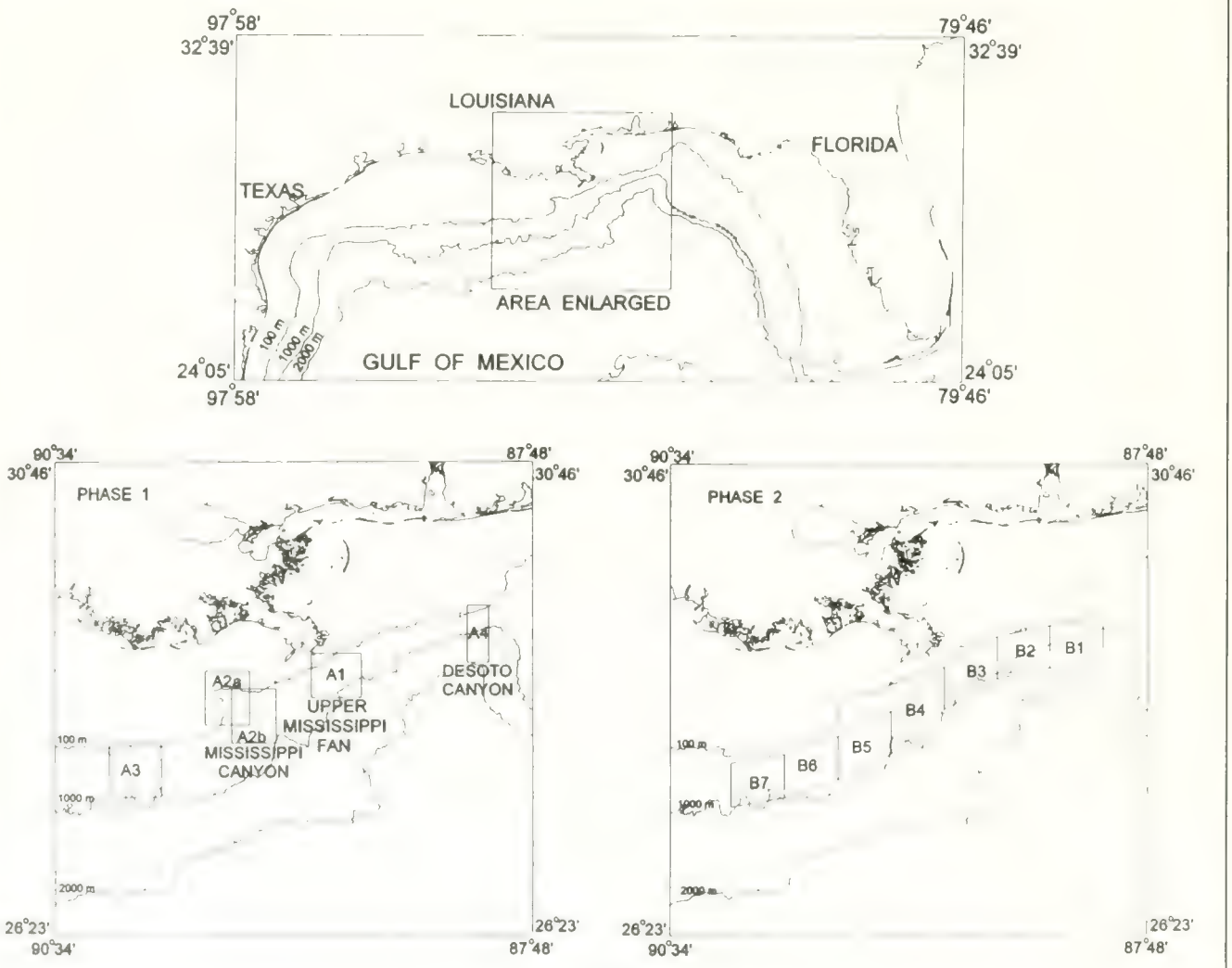

Figure 1

Location of the area surveyed for cetaceans in the north-central Gulf of Mexico (top panel). The locations of the survey blocks for Phase 1 (July–November 1989) are shown in the lower left panel and for Phase 2 (January–June 1990), in the lower right panel.

if any, inhabited the upper continental slope in the north-central Gulf. Since studies elsewhere indicated that cetaceans may concentrate in areas of high seafloor relief (Hui, 1979; Payne et al., 1986; Kenney and Winn, 1986; Selzer and Payne, 1988), three survey blocks were initially selected on the upper continental slope (Fig. 1, Blocks A1–A3; Table 1): 1) the Upper Mississippi Fan, 2) the Mississippi Canyon, and 3) an area of submarine salt domes. The DeSoto Canyon survey block (Block A4) was added in September when additional flight time was available.

The Mississippi Canyon survey block was shifted southeast to include deeper waters for the October and November surveys. This was done because sperm whales, *Physeter macrocephalus*, were sighted near the 1,000-m isobath during September in the Upper Mississippi Fan survey block. The sperm whale is listed as an endangered species under the U.S. Endangered Species Act (USFWS, 1989), and we were interested in defining its distribution.

The results of Phase 1 indicated that a variety of cetaceans were relatively abundant on the upper continental slope; ten species and 171 herds were sighted. Therefore, Phase 2 was implemented and monthly surveys, except for December, were continued to complete a full year period.

Phase 2 was conducted from January through June 1990. The study area selected for Phase 2 consisted of seven adjacent blocks 30 minutes wide (48.7 km) that extended from long. 87.5'W to long. 90.5'W (Fig. 1, Blocks B1–B7). The northern border of the study area, except near the Mississippi Canyon, generally followed the 200-m isobath. Each block extended 44.1 km south of its northern border.

The Mississippi Canyon was not surveyed because we wanted to focus on oceanic waters. Because of the shape of the canyon, surveys of oceanic waters would have been logistically inefficient. We also believed that the results of Phase 1 established the canyon as important cetacean habitat; eight species were identified in 54 sightings.

Aerial surveys were conducted when the sea state was Beaufort 0–4 and visibility was good and were designed to sample blocks A1–A4 at least twice each month during Phase 1, and blocks B1–B7 twice each month during Phase 2. Line transect sampling methods were used (Buckland et al., 1993) although line transect analyses are not presented here.

The survey aircraft, a DeHavilland Twin Otter with a large plexiglass bubble window on each side that allowed observers to view an area on both side of the transect line, was flown at an altitude of 750 feet (229 m) and a speed of 110 knots (204 km/h). Transects that were uniformly spaced from a random starting point were surveyed in each block (Table 1). Transects ran north-south, perpendicular to the bathymetry. One observer was stationed at each bubble window and one at a computer station. Observers rotated every 30 minutes to avoid fatigue. The bubble windows were divided into seven 10'

Table 1

Summary of area, water depth, transect length, number of transects, and effort per month for each survey block in the Gulf of Mexico.

					Transect kilometers of effort per month and block											
					1989					1990						
Block	Area (km^2)	Range of water depths (m)	Transect length (km)	Number of transects[1]	Jul	Aug	Sep	Oct	Nov	Jan	Feb	Mar	Apr	May	Jun	Total
A1	2,099	18–1,317	46.3	5	934	677	956	634	920	—			—	—	—	4,121
A2a	2,255	29–573	55.5	3	440	447	396	—	—	—	—	—	—			1,283
A2b	2,255	134–966	55.5	3	—	—	—	499	167	—	—	—	—	—	—	666
A3	2,640	104–1,152	55.5	3	394	489	412	0	164							1,459
A4	1,180	66–2,003	59.2	3	—	—	176	356	535	—	—	—	—	—	—	1,067
B1	2,160	168–1,792	44.1	4	—	—				0	179	362	362	269	265	1,437
B2	2,160	139–1,710	44.1	4	—	—	—	—	—	178	178	223	178	352	717	1,826
B3	2,160	163–1,070	44.1	4	—	—	—	—	—	357	176	631	360	445	449	2,418
B4	2,160	183–1,125	44.1	4	—	—	—	—	—	231	0	355	357	170	544	1,657
B5	2,160	230–979	44.1	4	—	—	—	—	—	128	0	358	360	361	361	1,568
B6	2,160	152–933	44.1	4	—	—	—	—	—	312	0	178	273	358	357	1,478
B7	2,160	176–1,098	44.1	4	—	—	—	—	—	356	0	180	361	354	362	1,613
				Total	1,768	1,613	1,940	1,489	1,786	1,562	533	2,287	2,251	2,309	3,055	20,593

[1] Number of planned transects each time the block was surveyed.

sighting intervals corresponding to perpendicular distances from the transect line of 40, 83, 132, 192, 273, 397, and 629 m. Observers searched on and near the transect line and scanned periodically out to 629 m. Sighting cues beyond 629 m were ignored unless the observer was certain it was a cetacean.

When cetaceans were encountered, the sighting interval was noted and the herd was circled. Before continuing on the transect, the herd was identified and its size estimated. The identifying characteristics of each cetacean species were noted. Data were entered on a computer interfaced with a LORAN-C navigation receiver. Latitude, longitude, and heading were automatically recorded with each data record.

Cetaceans were identified to the lowest taxonomic level possible from descriptions in field guides by Leatherwood et al. (1976) and Leatherwood and Reeves (1983). Our ability to make an identification was dependent on water clarity, sea state, and animal behavior. We were not able to distinguish species of some genera or groups of species. These groups included 1) the species of *Mesoplodon*; 2) the melon-headed whale, *Peponocephala electra*, and pygmy killer whale, *Feresa attenuata*; 3) the dwarf sperm whale, *Kogia simus*, and pygmy sperm whale, *K. breviceps*; and 4) the short-finned pilot whale, *Globicephala macrorhynchus*, and long-finned pilot whale,[4] *G. melaena*. Cuvier's beaked whale, *Ziphius cavirostris*, and *Mesoplodon* spp. could not always be distinguished and these sightings were classified as unidentified ziphiids. While we did make positive identifications of striped dolphins, *S. coeruloealba*, spinner dolphins, *S. longirostris*, and clymene dolphins, *S. clymene*, from photographs, they were usually difficult to distinguish in the field and were grouped together for analyses. In some cases, animals could only be identified as large cetaceans (greater than about 7 m) or small cetaceans (less than about 7 m).

For species or species groups sighted 20 or more times, the null hypothesis that water depth did not vary among species or species groups was tested with one-way analysis of variance. If the null hypothesis was rejected, Duncan's multiple-range test was used to determine where significant differences in mean water depths occurred.

Sighting rates of herds and individuals were used as measures of overall, temporal, and spatial relative abundance. Seasons were defined as summer (June–August), fall (September–November), winter (January–February), and spring (March–May). To summarize spatial relative abundance, the area surveyed was divided into an eastern zone (Blocks A4, B1, and B2), a central zone (Blocks A1, A2, B3, B4, and B5), and a western zone (Blocks A3, B6, and B7). All sightings from each season and zone were pooled. For each season and for each zone, the sighting rate of herds (herds/100 transect km) and animals (animals/100 transect km) of each species or species group was calculated.

We also compared the relative abundance of individuals of each species or species group from our surveys to those from the Gulf stranding database (Mead[3]). The database of Gulf strandings contained 2,321 records identified to species. Only 516 records (22%) were not those of bottlenose dolphins. To compare our results with these data, we excluded bottlenose dolphins and unidentified cetaceans from both data sets. We used our species or species-group categories and calculated the relative abundance of each within each data set as a percentage of the total number of animals.

Results

In total, we sighted 320 herds (7,438 animals) and identified 18 species of cetaceans (Table 2); 45 herds (14%) could not be identified. Of the 275 identified herds (6,084 animals), 93.5% of the herds and 97.7% of the animals consisted of seven species or species groups: Risso's dolphins (herds, 22.2%; animals, 12.6%); sperm whales (15.6%, 1.4%); bottlenose dolphins (14.2%, 7.4%); Atlantic spotted dolphins (12.8%, 15.0%); pygmy and dwarf sperm whales (11.6%, 1.0%); striped, spinner, and clymene dolphins (8.7%, 33.8%); and pantropical spotted dolphins (8.4%, 26.5%).

Mean herd sizes of species or species groups sighted more than 20 times ranged from 1.9 to 87.8 animals (Table 2). The largest herd consisted of 325 striped, spinner, or clymene dolphins (SSC dolphins). Dolphins of the genus *Stenella* had the largest mean herd sizes and the largest ranges of herd sizes. However, the mean herd sizes of pantropical spotted dolphins and SSC dolphins were each about three times that of the Atlantic spotted dolphin. The mean herd sizes of sperm whales and pygmy and dwarf sperm whales were close to two, and they exhibited the smallest ranges of herd sizes. Bottlenose dolphins and Risso's dolphins had similar means and ranges of herd sizes.

Mean water depths of species or species groups sighted 20 or more times ranged from 257 to 905 m (Table 2). Differences between these means were statistically significant (Table 3). Mean water depths of pantropical spotted dolphin, sperm whale, and SSC dolphin sightings were the largest (>700 m). Each of

[4] Only the short-finned pilot whale is known to inhabit the Gulf of Mexico (Schmidly, 1981).

Table 2

Cetaceans sighted, mean herd size (H) and mean water depth ($\bar{W}$; n = number of herds) from aerial surveys conducted in the Gulf of Mexico from July 1989 to June 1990 (%CV=percent coefficient of variation).

		Herd size (animals)			Water depth (meters)			
Species or species group	n	H	SE	Range	W	SE	Range	%CV
Risso's dolphin (*Grampus griseus*)	61	12.8	1.46	1–48	440	25.5	97–1,079	46
Sperm whale (*Physeter macrocephalus*)	43	2.1	0.30	1–9	877	35.5	199–1,573	27
Bottlenose dolphin (*Tursiops truncatus*)	39	11.9	2.23	1–60	257	41.0	20–973	100
Atlantic spotted dolphin (*Stenella frontalis*)	35	26.6	5.15	2–137	367	40.3	91–1,152	65
Pygmy/dwarf sperm whales (*Kogia breviceps/simus*)	32	1.9	0.20	1–4	544	63.8	96–1,780	65
SSC dolphins[1] (*S. coeruleoalba/longirostris/clymene*)	24	87.8	20.44	8–325	712	76.3	93–1,567	53
Pantropical spotted dolphin (*S. attenuata*)	23	71.8	9.38	7–186	905	76.6	65–1,566	39
Pilot whale (*Globicephala* sp.)	5	18.2	3.73	5–28	605	71.3	364–781	28
Cuvier's beaked whale (*Ziphius cavirostris*)	3	1.3	0.33	1–2	1,268	275.1	916–1,810	38
Mesoplodon sp.	1	1.0	—	—	910	—	—	—
Unidentified ziphiids (*Mesoplodon/Ziphius*)	3	1.3	0.33	1–2	668	238.2	204–993	62
Pygmy killer/melon-headed whales (*Feresa/Peponocephala*)	1	25.0	—	—	318	—	—	—
False killer whale (*Pseudorca crassidens*)	1	3.0	—	—	1,107	—	—	—
Killer whale (*Orcinus orca*)	1	8.0	—	—	964	—	—	—
Rough-toothed dolphin (*Steno bredanensis*)	1	4.0	—	—	933	—	—	—
Fin whale (*Balaenoptera physalus*)	1	1.0	—	—	148	—	—	—
Bryde's whale (*B. edeni*)	1	1.0	—	—	342	—	—	—
Unidentified small cetacean	40	30.1	10.38	1–325	530	68.3	87–1,779	82
Unidentified large cetacean	5	1.8	0.45	1–3	857	288.2	316–1,673	57

[1] S. *coeruleoalba*, *S. longirostris*, and *S. clymene* were each positively identified at least once.

these species inhabited a range of water depths greater than 1,300 m. However, most sperm whales inhabited a very narrow range of water depths (Fig. 2). The mean depth of sperm whale sightings had a coefficient of variation of 0.27, the lowest of any species or species group (Table 3). Bottlenose dolphins, Atlantic spotted dolphins, and Risso's dolphins had the shallowest mean water depths (<450 m) and inhabited a range of water depths less than 1,100 m. Cuvier's beaked whales were only sighted at depths greater than 900 m.

Cetaceans were widely distributed between seasons (Table 4). Five species or species groups were sighted in every season of the year: sperm whales, bottlenose dolphins, Risso's dolphins, Atlantic spotted dolphins, and SSC dolphins. Pygmy and dwarf sperm whales and pantropical spotted dolphins were sighted in all seasons except winter and Cuvier's beaked whale,

Table 3

Duncan's multiple range test of mean water depths (W) inhabited by cetacean species and species groups in the Gulf of Mexico during 1989–90 (ANOVA: F=29.3, P<0.05; species or species groups sighted more than 20 times; n=number of herds).

Species or species group	n	W (meters)	Duncan grouping*
Pantropical spotted dolphin (*Stenella attenuata*)	23	905	A
Sperm whale (*Physeter macrocephalus*)	43	877	A
SSC dolphins (*S. coeruleoalba/ longirostris/clymene*)	24	712	B
Pygmy/dwarf sperm whales (*Kogia breviceps/simus*)	32	544	C
Risso's dolphin (*Grampus griseus*)	61	440	C D
Atlantic spotted dolphin (*S. frontalis*)	36	368	D E
Bottlenose dolphin (*Tursiops truncatus*)	39	257	E

* Means with the same letter are not significantly different, P>0.05.

in all seasons except summer. The number of species or species groups sighted in summer, fall, winter and spring was 12, 10, 6, and 10, respectively. Seasonal sighting rates of all cetacean herds ranged from 0.91 herds/100 km (winter) to 2.01 herds/100 km (fall) and those of all animals sighted ranged from 16.80 animals/100 km (summer) to 52.25 animals/100 km (fall).

The relative abundance of several species or species groups varied seasonally (Table 4). Sighting rates (herds and animals) of Risso's dolphins showed a distinct peak during spring. During April alone, 30% of the Risso's dolphin herds and 48% of the animals were sighted. Sighting rates of sperm whales and Atlantic spotted dolphins peaked in the fall. Sighting rates of bottlenose dolphins and pygmy and dwarf sperm whales were highest during summer and fall. SSC dolphins exhibited similar herd sighting rates in each season, but the animal sighting rate was much lower during summer. SSC dolphin herds averaged only about 20 animals in summer but near 100 or more during other seasons.

Cetaceans were sighted throughout the area surveyed (Fig. 2). Each species or species group sighted 20 or more times had a wide spatial distribution and was sighted in all three zones (Fig. 2, Table 5). Ten species were sighted in the eastern zone, 13 in the central zone, and nine in the western zone. Sighting rates of all herds sighted were generally similar in the eastern and central zones (1.67 and 1.71 herds/100 km, respectively) and a little lower in the western zone (1.05 herds/100 km). However, because the mean herd size of all cetaceans sighted from the eastern zone (35.8 animals) was larger than those of the central (19.2 animals) and western (21.5 animals) zones, the sighting rates of animals were more variable: 59.5 animals/100 km (eastern), 32.7 animals/100 km (central), and 22.6 animals/100 km (western).

Sighting rates of species or species groups sighted 20 or more times varied by zone (Table 5). Except for Atlantic spotted dolphins and pantropical spotted dolphins, herd sighting rates were lowest in the western zone. Except for pantropical spotted dolphins, the animal sighting rates were also lowest in the western zone. Sighting rates (herd and animal) of Risso's dolphins and SSC dolphins were highest in the eastern zone. In the central zone, sighting rates of sperm whales, bottlenose dolphins, Atlantic spotted dolphins, and pygmy and dwarf sperm whales were highest; those of pantropical spotted dolphins were lowest.

Risso's dolphin sightings in the eastern part of the study area were generally concentrated near the 200-m isobath. Most of the sperm whale sightings (65%) occurred southeast of the Mississippi River delta along the 1,000-m isobath. Of 39 bottlenose dolphin herds sighted, 19 were sighted in waters less than 100 m deep, at the head of the Mississippi Canyon and on the Upper Mississippi Fan. A concentration of pygmy and dwarf sperm whales occurred along the western Mississippi Canyon. Most of the SSC dolphin sightings occurred on the Upper Mississippi Fan and in DeSoto Canyon. Four of the five pilot whale herds sighted were encountered on the Upper Mississippi Fan on 4 November 1989. The only baleen whales sighted, one fin whale, *Balaenoptera physalus*, in the fall and one Bryde's whale, *B. edeni*, in the summer, were both sighted in waters about 200 m deep in the DeSoto Canyon (Fig. 2).

The relative abundance of many species or species groups was different from the Gulf stranding data (Table 6). Compared with the stranding database, the relative abundances of Risso's dolphins, pantropical spotted dolphins, and Atlantic spotted dolphins were greater in our study. The relative abundances of balaenopterid whales, ziphiids, pilot whales, and pygmy and dwarf sperm whales from the stranding data were larger than those observed during our surveys.

Discussion

This study was the first to focus on cetaceans in the oceanic Gulf of Mexico. We sighted at least 18 of the 29 cetacean species with one or more historical

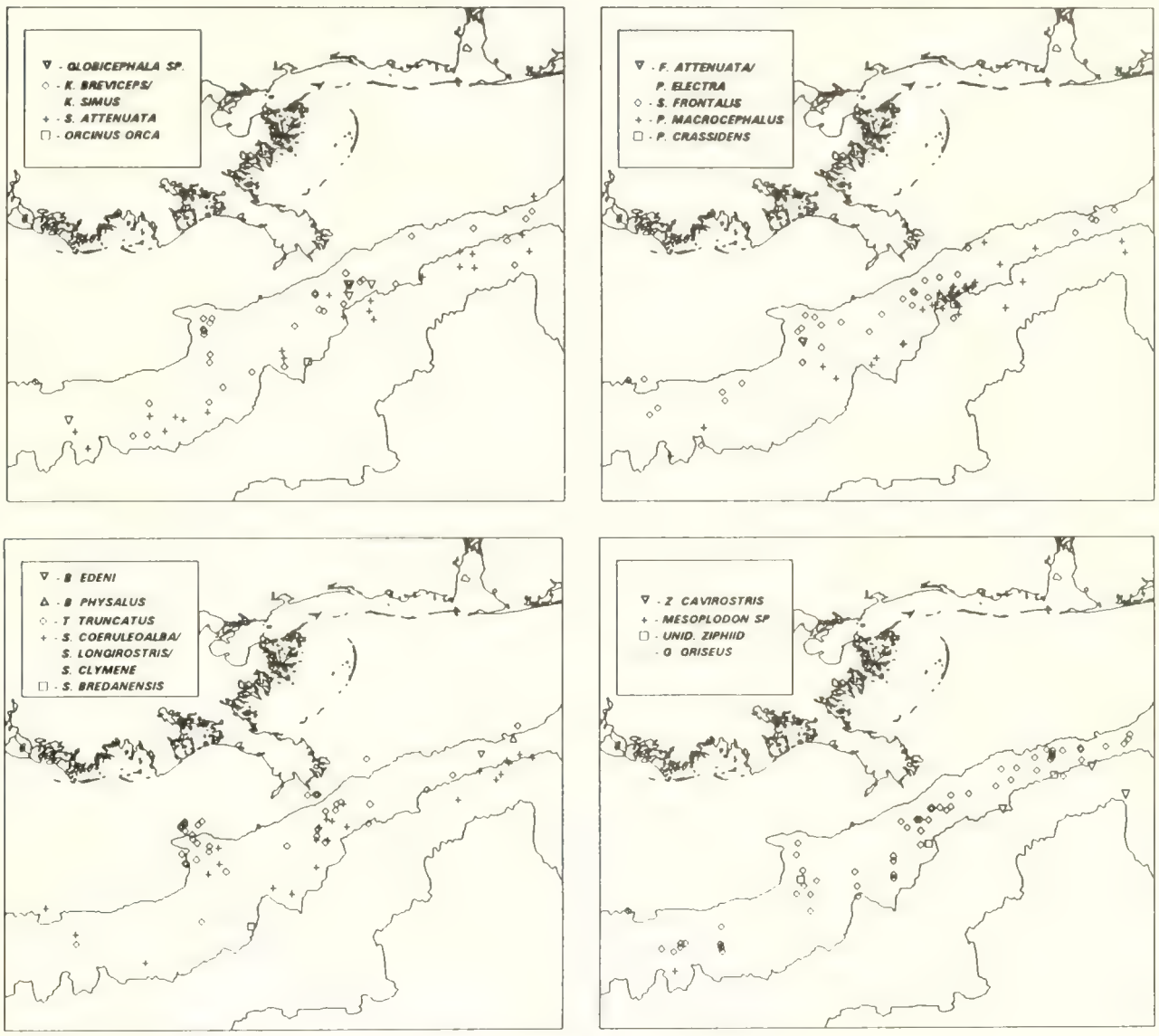

Figure 2

The locations of sightings of each cetacean species or species group in the Gulf of Mexico for the entire study (July 1989–June 1990).

records from the Gulf. The first at-sea identifications of Bryde's whale, pygmy and dwarf sperm whales, spinner dolphins, and Cuvier's beaked whales in the Gulf were recorded during this study. Prior to this study, species with five or fewer herd-sighting records (nonstranding) from the Gulf included pantropical spotted dolphin, clymene dolphin, Risso's dolphin, killer whale, false killer whale, rough-toothed dolphin, fin whale, pygmy killer whale, melon-headed whale, and *Mesoplodon* spp. (Schmidly, 1981; Jennings, 1982; Fritts et al., 1983; Rademacher[2]). Sperm whales were hunted commercially in the Gulf until the early 1900's (Townsend, 1935) but were recently thought to be rare (Lowery, 1974). However, our data and the 17 Gulf sperm whale sightings reported by Collum and Fritts (1985) indicate they may be more abundant than previously thought. Species known from the Gulf that could be distinguished from aircraft, but were not identified during our surveys, included the northern right whale, *Eubalaena glacialis*, the blue whale, *B. musculus*, the minke whale, *B. acutorostrata*, the humpback whale, *Megaptera novaeangliae*, and the Fraser's dolphin, *Lagenodelphis hosei*.

Table 4

Seasonal sighting rates of cetacean herds (herds/100 km) and individual animals (animals/100 km) in the Gulf of Mexico during 1989–90. The effort in transect km each season is in parentheses (h=number of herds sighted; a=number of animals sighted).

	Summer (6,436 km)		Fall (5,215 km)		Winter (2,095 km)		Spring (6,847 km)		Total (20,593 km)	
Species or species group	Herds (h)	Animals (a)	Herds (h)	Animals (a)	Herds (h)	Animals (a)	Herds (h)	Animals (a)	Herds (h)	Animals (a)
All cetaceans	1.46 (94)	16.80 (1,081)	2.01 (105)	52.25 (2,749)	0.91 (19)	32.12 (673)	1.49 (102)	42.87 (2,935)	1.55 (320)	36.12 (7,438)
Risso's dolphin (*Grampus griseus*)	0.26 (17)	2.63 (169)	0.06 (3)	1.00 (52)	0.10 (2)	1.53 (32)	0.57 (39)	7.73 (529)	0.29 (61)	3.80 (782)
Sperm whale (*Physeter macrocephalus*)	0.11 (7)	0.34 (22)	0.46 (24)	1.04 (54)	0.29 (6)	0.33 (7)	0.09 (6)	0.09 (6)	0.21 (43)	0.43 (89)
Bottlenose dolphin (*Tursiops truncatus*)	0.28 (18)	2.41 (155)	0.33 (17)	4.93 (257)	0.10 (2)	2.10 (44)	0.03 (2)	0.10 (7)	0.19 (39)	2.25 (463)
Atlantic spotted dolphin (*Stenella frontalis*)	0.12 (8)	2.41 (155)	0.31 (16)	11.03 (575)	0.10 (2)	2.10 (44)	0.13 (9)	2.31 (158)	0.17 (35)	4.53 (932)
Pygmy/dwarf sperm whales (*Kogia breviceps/simus*)	0.19 (12)	0.37 (24)	0.23 (12)	0.46 (24)	0	0	0.12 (8)	0.19 (13)	0.16 (32)	0.30 (61)
SSC dolphins (*S. coeruleoalba/ longirostris/clymene*)	0.12 (8)	2.42 (156)	0.12 (6)	11.43 (596)	0.14 (3)	25.78 (540)	0.10 (7)	11.89 (814)	0.12 (24)	10.23 (2,106)
Pantropical spotted dolphin (*S. attenuata*)	0.08 (5)	4.29 (276)	0.13 (7)	10.26 (535)	0	0	0.16 (11)	12.27 (840)	0.11 (23)	8.02 (1,651)
Pilot whale (*Globicephala* sp.)	0.02 (1)	0.08 (5)	0.08 (4)	1.65 (86)	0	0	0	0	0.02 (5)	0.44 (91)

Continued on next page

The ecological implications of Gulf stranding records are not clear since there are only a small number of strandings of most species. It is not known whether the stranded animals strayed into the Gulf from their primary ranges or whether they inhabited Gulf waters on a regular basis. The number and broad seasonality of sightings during this study of Risso's dolphins, sperm whales, pygmy and dwarf sperm whales, SSC dolphins, and pantropical spotted dolphins indicate that they are probably permanent residents of the Gulf.

How accurately our results reflected the abundance of each species relative to other species is uncertain. Factors that vary among species, such as surface behavior, herd size, and time spent at or near the surface, can affect sighting rates. In our study, water depth or area, or both (e.g. Mississippi Canyon), affected the distribution of some species. However, our survey effort was not equal seasonally over water depths or by area and this probably affected at least some of our relative abundance results (Tables 4–5). Forty-nine percent (19/39) of the bottlenose dolphin herds we sighted were encountered during summer and fall at the head of the Mississippi Canyon and on the Upper Mississippi Fan at depths less than 100 m. (Survey effort at <100 m made up <5% of the total effort, 8.5% of both the summer and fall effort, and 0% of the winter and spring effort.) Without these sightings, the seasonal sighting rates of bottlenose dolphins were less variable. Also, 28% (9/32) of the pygmy and dwarf sperm whale sightings and 26% (9/35) of the Atlantic spotted dolphin sightings occurred in the Mississippi Canyon (Block A2, surveyed during summer and fall) where only

Table 4 (Continued)

Species or species group	Summer (6,436 km) Herds (h)	Summer (6,436 km) Animals (a)	Fall (5,215 km) Herds (h)	Fall (5,215 km) Animals (a)	Winter (2,095 km) Herds (h)	Winter (2,095 km) Animals (a)	Spring (6,847 km) Herds (h)	Spring (6,847 km) Animals (a)	Total (20,593 km) Herds (h)	Total (20,593 km) Animals (a)
Cuvier's beaked whale (*Ziphius cavirostris*)	0	0	0.02 (1)	0.02 (1)	0.05 (1)	0.05 (1)	0.01 (1)	0.03 (2)	0.01 (3)	0.02 (4)
Mesoplodon sp.	0.02 (1)	0.02 (1)	0	0	0	0	0	0	<0.01 (1)	<0.01 (1)
Unidentified ziphiids (*Mesoplodon/Ziphius*)	0.02 (1)	0.03 (2)	0.02 (1)	0.02 (1)	0	0	0.01 (1)	0.01 (1)	0.01 (3)	0.02 (4)
Pygmy killer/melon-headed whales (*Feresa/Peponocephala*)	0.02 (1)	0.39 (25)	0	0	0	0	0	0	<0.01 (1)	0.12 (25)
False killer whale (*Pseudorca crassidens*)	0.02 (1)	0.05 (3)	0	0	0	0	0	0	<0.01 (1)	0.01 (3)
Killer whale (*Orcinus orca*)	0	0	0	0	0	0	0.01 (1)	0.12 (8)	<0.01 (1)	0.04 (8)
Rough-toothed dolphin (*Steno bredanensis*)	0	0	0	0	0	0	0.01 (1)	0.06 (4)	<0.01 (1)	0.02 (4)
Fin whale (*Balaenoptera physalus*)	0	0	0.02 (1)	0.02 (1)	0	0	0	0	<0.01 (1)	<0.01 (1)
Bryde's whale (*B. edeni*)	0.02 (1)	0.02 (1)	0	0	0	0	0	0	<0.01 (1)	<0.01 (1)
Unidentified large cetacean	0	0	0.02 (1)	0.06 (3)	0.05 (1)	0.05 (1)	0.04 (3)	0.07 (5)	0.02 (5)	0.04 (9)
Unidentified small cetacean	0.20 (13)	1.35 (87)	0.23 (12)	10.81 (564)	0.10 (2)	0.19 (4)	0.19 (13)	8.00 (548)	0.19 (40)	5.84 (1,203)

10% of the total survey effort occurred. The Mississippi Canyon region is probably an important cetacean habitat. Eight species or species groups were sighted there and when herd sighting rates were calculated for each survey block (Mullin et al.[5]), it had the highest sighting rate of any block.

The region near the 1,000-m isobath on the Upper Mississippi Fan appeared to be an important habitat for sperm whales. Most sperm whale herd sightings (72%, 31/43) occurred on the Upper Mississippi Fan (Blocks A1, B3, and B4) but only 40% of the total effort occurred there. Fall may have been a time of increased sperm whale abundance on the Upper Mississippi Fan. Of the total effort, 20% occurred in fall on the Upper Mississippi Fan and yielded 47% (20/43) of the total sperm whale herd sightings. Of course the same animals could have been seen repeatedly, but even if that were true, it indicates that a very small area (Fig. 2) could be important to some animals for a period of at least several months.

Our study was confined to the outer continental shelf and the upper continental slope and did not cover the entire range of water depths that each species inhabits. However, our results do not conflict with what is generally known about the water depth distribution of each species (Leatherwood and Reeves, 1983). While the supposition that only bottlenose dolphins and Atlantic spotted dolphins inhabit

[5] Mullin, K., W. Hoggard, C. Roden, R. Lohoefener, C. Rogers, and B. Taggart. 1991. Cetaceans on the upper continental slope in the north-central Gulf of Mexico. Outer Continental Shelf Study/MMS 91-0027. U.S. Dep. Interior, Minerals Mgmt. Service, Gulf of Mexico OCS Regional Office, New Orleans, LA, 108 p.

Table 5

Sighting rates of cetacean herds (herds/100 km) and animals (animals/100 km) by zone (Fig. 2: Eastern=blocks A4, B1 and B2; Central=A1, A2, B3, B4 and B5; Western=A3, B6 and B7) in the Gulf of Mexico during 1989–90. Effort in kilometers in each zone is in parentheses (h=number of herds, a=number of animals).

Species or species group	Eastern (4,330 km)		Central (11,713 km)		Western (4,550 km)	
	Herds (h)	Animals (a)	Herds (h)	Animals (a)	Herds (h)	Animals (a)
All cetaceans	1.67 (72)	59.54 (2,578)	1.71 (200)	32.70 (3,830)	1.05 (48)	22.64 (1,030)
Risso's dolphin (*Grampus griseus*)	0.51 (22)	7.39 (320)	0.25 (29)	3.04 (356)	0.22 (10)	2.33 (106)
Sperm whale (*Physeter macrocephalus*)	0.14 (6)	0.18 (8)	0.30 (35)	0.67 (79)	0.04 (2)	0.04 (2)
Bottlenose dolphin (*Tursiops truncatus*)	0.07 (3)	1.39 (60)	0.29 (34)	2.95 (346)	0.04 (2)	1.25 (57)
Atlantic spotted dolphin (*Stenella frontalis*)	0.09 (4)	4.32 (187)	0.20 (23)	5.20 (609)	0.18 (8)	2.99 (136)
Pygmy/dwarf sperm whales (*Kogia breviceps/simus*)	0.14 (6)	0.30 (13)	0.19 (22)	0.34 (40)	0.09 (4)	0.18 (8)
SSC dolphins (*S. coeruleoalba/ longirostris/clymene*)	0.18 (8)	22.96 (994)	0.11 (13)	8.81 (1,032)	0.07 (3)	1.76 (80)
Pantropical spotted dolphin (*S. attenuata*)	0.18 (8)	9.63 (417)	0.08 (9)	5.43 (636)	0.13 (6)	13.14 (598)
Pilot whale (*Globicephala* sp.)	0	0	0.03 (4)	0.73 (86)	0.02 (1)	0.11 (5)
Cuvier's beaked whale (*Ziphius cavirostris*)	0.07 (3)	0.09 (4)	0	0	0	0

Continued on next page

most continental shelf waters of the U.S. Gulf (Lowery, 1974; Scott et al.[1]; Rademacher[2]) may be true, we did sight Risso's dolphins, pygmy and dwarf sperm whales, SSC dolphins, pantropical spotted dolphins, and a sperm whale at depths less than 200 m. Fritts et al. (1983) identified a sperm whale and SSC dolphins on the continental shelf off southern Florida.

In general, our results of mean herd size for most species were similar to those reported from the Atlantic and Pacific oceans (Yamada, 1954; Ross, 1978; Leatherwood et al., 1980; Fritts et al., 1983; Leatherwood and Reeves, 1983; Vidal et al., 1987; Scott and Cordaro, 1987; Kruse, 1989; Wade and Gerrodette, 1993; CeTAP[6]). Our mean herd size for sperm whales (2.1 animals) was slightly smaller than the mean of 3.5 animals reported by Collum and Fritts (1985) from Gulf sightings. However, in other areas of the world, mixed-sex herds and bachelor herds of sperm whales range from 20 to 40 whales (Rice, 1989).

The maximum herd sizes reported from the Atlantic and Pacific oceans were much greater than those observed in this study, where the largest herd was estimated at 325 animals. Maximum herd sizes of Risso's dolphins, bottlenose dolphins, striped dol-

[6] CeTAP. 1982. A characterization of marine mammals and turtles in the mid- and north-Atlantic areas of the U.S. outer continental shelf. Final Report of the Cetacean and Turtle Assessment Program, BLM Contract AA551-CT8-48, U.S. Dep. Interior, Washington D.C., 450 p.

Table 5 (Continued)

Species or species group	Eastern (4,330 km)		Central (11,713 km)		Western (4,550 km)	
	Herds (*h*)	Animals (*a*)	Herds (*h*)	Animals (*a*)	Herds (*h*)	Animals (*a*)
Mesoplodon sp.	0	0	0	0	0.02 (1)	0.02 (1)
Unidentified ziphiids (*Mesoplodon/Ziphius*)	0.02 (1)	0.02 (1)	0.02 (2)	0.03 (3)	0	0
Pygmy killer/melon-headed whales (*Feresa/Peponocephala*)	0	0	<0.01 (1)	0.21 (25)	0	0
False killer whale (*Pseudorca crassidens*)	0	0	<0.01 (1)	0.03 (3)	0	0
Killer whale (*Orcinus orca*)	0	0	<0.01 (1)	0.07 (8)	0	0
Rough-toothed dolphin (*Steno bredanensis*)	0	0	<0.01 (1)	0.03 (4)	0	0
Fin whale (*Balaenoptera physalus*)	0.02 (1)	0.02 (1)	0	0	0	0
Bryde's whale (*B. edeni*)	0.02 (1)	0.02 (1)	0	0	0	0
Unidentified large cetacean	0.05 (2)	0.09 (4)	0.02 (2)	0.02 (2)	0.02 (1)	0.07 (3)
Unidentified small cetacean	0.16 (7)	13.12 (568)	0.20 (23)	5.13 (601)	0.22 (10)	0.75 (34)

phins, and pilot whales in the Atlantic exceeded 350 animals (CeTAP[6]). Herds of striped dolphins, pantropical spotted dolphins, and spinner dolphins exceeding 1,000 animals in the Pacific are not uncommon (Leatherwood and Reeves, 1983). In Monterey Bay, California, Risso's dolphin herds as large as 500 animals have been reported (Kruse, 1989). These differences in maximum herd sizes may be related to how prey or predators, or both, are distributed in these areas (Norris and Dohl, 1980; Wells et al., 1980).

We sighted two mixed species herds (Risso's dolphins and pilot whales; Atlantic spotted and bottlenose dolphins). Fritts et al. (1983) reported only three mixed species herds in the Gulf: two herds of pilot whales and *Stenella* sp., and one herd of Risso's dolphins with an unidentified whale. Risso's dolphins are often associated with other oceanic cetaceans (Leatherwood and Reeves, 1983; Kruse, 1989). In the eastern tropical Pacific, spinner and pantropical spotted dolphins are commonly found together (Au and Perryman, 1985). Bottlenose dolphins were associated with other species (primarily pilot whales) in 20% of the sightings in the Pacific (Scott and Chivers, 1990). While we sighted only five herds of pilot whales, other species that are commonly in mixed species herds elsewhere (Risso's dolphins, bottlenose dolphins, and pantropical spotted dolphins), accounted for 44% of our identified herd sightings. The abundance and distribution of prey or predators, or both, may be factors involved in the formation of mixed species herds (see Scott and Chivers, 1990). There may be differences in these factors in the Gulf of Mexico compared with those in the northwestern Atlantic and Pacific oceans.

The abundance of prey species has been demonstrated to be positively correlated with the abundance of several species of cetaceans (e.g. Kenney and Winn, 1986; Payne et al., 1986; Selzer and Payne, 1988). Fish and squid are the primary prey of most odon-

tocetes (e.g. Clarke, 1986; Barros and Odell, 1990; Sekiguchi et al., 1992). However, very little is known about the distribution and abundance of potential prey species in Gulf oceanic waters beyond limited information on cephalopods (e.g. Voss, 1971; Voss and Brakoniecki, 1985) and records of the presence of species (e.g. Hoese et al., 1977).

Oceanographic features undoubtedly affect the distribution of prey species and, ultimately, cetacean diversity, abundance, and distribution. The Mississippi River and its distributary, the Atchafalaya River, enter the Gulf north of the area we surveyed and account for nearly one-half of the total freshwater flow into the entire Gulf. The Loop Current, the major oceanographic feature in the eastern Gulf, carries 25–30 million m^3 of water per second into the Gulf. At times, the Loop Current extends as far north as the Upper Mississippi Fan or the DeSoto Canyon. As the Loop Current flows onto the continental slope it causes nutrient-rich upwellings (Jones et al., 1973; Weber et al., 1990). All these features interact with the diverse bottom topography of the north-central Gulf, making it a very dynamic area.

In 1990, the Southeast Fisheries Science Center began conducting annual cetacean shipboard surveys of the entire oceanic U.S. Gulf of Mexico. Results to date (775 herd sightings) suggest that the comparatively small maximum herd sizes and single species herds found in this study in the Gulf are accurate (SEFSC[7]). Comparisons of the ecology of Gulf cetaceans with those from other areas should provide an excellent opportunity to understand the physical and biological factors that affect cetacean diversity, distribution, abundance, herd sizes, and associations.

Table 6

Comparison of relative abundances of cetaceans determined by aerial counts during 1989–90 and by historical strandings in the Gulf of Mexico.

Species or species group	Strandings[1]	This study
Balaenopterids	9.3% (48)	<0.1% (2)
Sperm whale (*Physeter macrocephalus*)	4.7% (24)	1.5% (89)
Pygmy/dwarf sperm whales (*Kogia breviceps/simus*)	15.3% (79)	1.1% (61)
Unidentified ziphiids (*Mesoplodon/Ziphius*)	10.6% (55)	0.2% (9)
Risso's dolphin (*Grampus griseus*)	2.7% (14)	13.6% (782)
Atlantic spotted dolphin (*Stenella frontalis*)	7.0% (36)	16.2% (932)
Pantropical spotted dolphin (*S. attenuata*)	1.4% (7)	28.6% (1,651)
SSC dolphins[1] (*S. coeruleoalba/ longirostris/clymene*)	22.3% (115)	36.5% (2,106)
Pilot whale (*Globicephala* sp.)	16.5% (85)	1.6% (91)
Pygmy killer/ melon-headed whales (*Feresa/Peponocephala*)	3.1% (16)	0.4% (25)
False killer whale (*Pseudorca crassidens*)	3.5% (18)	<0.1% (3)
Killer whale (*Orcinus orca*)	0.6% (3)	0.1% (8)
Rough-toothed dolphin (*Steno bredanensis*)	2.9% (15)	<0.1% (4)
Fraser's dolphin (*Lagenodelphis hosei*)	0.2% (1)	0%

[1] See Footnote 3.

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Literature cited

Au, D. W., and W. L. Perryman.
1985. Dolphin habitats in the eastern tropical Pacific. Fish. Bull. 83:623–643.

Barron, G. L., and T. A. Jefferson.
1993. First records of the melon-headed whale (*Peponocephala electra*) from the Gulf of Mexico. Southwest. Nat. 38:82–85.

[7] SEFSC. 1990–93. Reports of NOAA ship *Oregon II* cruises 187, 194, 199, 203, and 204. U.S. Dep. Commer., NOAA, Nat. Mar. Fish. Serv., Southeast Fish. Sci. Cent. Pascagoula Facility, P.O. Drawer 1207, Pascagoula, MS 39568.

Barros, N. B., and D. K. Odell.
1990. Food habits of bottlenose dolphins in the southeastern United States. *In* S. Leatherwood and R. R. Reeves (eds.), The bottlenose dolphin, p. 309–328. Academic Press, San Diego, CA.

Bonde, R. K., and T. J. O'Shea.
1989. Sowerby's beaked whale (*Mesoplodon bidens*) in the Gulf of Mexico. J. Mammal. 70:447–449.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake.
1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, 446 p.

Clarke, M. R.
1986. Cephalopods in the diet of odontocetes. *In* M. M. Bryden and R. Harrison (eds.), Research on dolphins, p. 281–321. Oxford Sci. Pub.

Collum, L. A., and T. H. Fritts.
1985. Sperm whales (*Physeter catodon*) in the Gulf of Mexico. Southwest. Nat. 30:101–104.

Fritts, T. H., A. B. Irvine, R. D. Jennings, L. A. Collum, W. Hoffman, and M. A. McGehee.
1983. Turtles, birds, and mammals in the northern Gulf of Mexico and nearby Atlantic waters. U.S. Fish and Wildl. Serv., Div. Biol. Serv., Washington, D.C. FWS/OBS-82/65, 455 p.

Gore, R. H.
1992. The Gulf of Mexico: a treasury of resources in the American Mediterranean. Pineapple Press, Sarasota, FL, 384 p.

Hersh, S. L., and D. K. Odell.
1986. Mass stranding of Fraser's dolphin, *Lagenodelphis hosei*, in the western North Atlantic. Mar. Mamm. Sci. 2:73–76.

Hoese, H. D., R. H. Moore, and V. F. Sonnier.
1977. Fishes of the Gulf of Mexico: Texas, Louisiana, and adjacent waters. Texas A&M Univ. Press, College Station, 327 p.

Hui, C. A.
1979. Undersea topography and distribution of dolphins of the genus *Delphinus* in the Southern California Bight. J. Mammal. 60:521–527.

Jennings, R.
1982. Pelagic sightings of Risso's dolphin, *Grampus griseus*, in the Gulf of Mexico and Atlantic Ocean adjacent to Florida. J. Mammal. 63:522–523.

Jones, J. I., R. E. Ring, M. O. Rinkel, and R. E. Smith.
1973. A summary of the knowledge of the eastern Gulf of Mexico. The State Univ. System of Florida, Institute of Oceanography, Gainsville, FL.

Kenney, R. D., and H. E. Winn.
1986. Cetacean high-use habitats of the northeast United States continental shelf. Fish. Bull. 84:345–357.

Kruse, S.L.
1989. Aspects of the biology, ecology and behavior of Risso's dolphin (*Grampus griseus*) off the California coast. M.S. thesis, Univ. Calif., Santa Cruz, 120 p.

Leatherwood, S., D. K. Caldwell, and H. E. Winn.
1976. Whales, dolphins, and porpoises of the western North Atlantic, a guide to their identification. NOAA Tech. Rep. NMFS CIRC-396, 176 p.

Leatherwood, S., W. F. Perrin, V. L. Kirby, C. L. Hubbs, and M. Dahlheim.
1980. Distribution and movements of Risso's dolphin, *Grampus griseus*, in the eastern North Pacific. Fish. Bull. 77:951–963.

Leatherwood, S., and R. R. Reeves.
1983. The Sierra Club handbook of whales and dolphins. Sierra Club Books, San Francisco, CA, 302 p.

Lowery, G. H., Jr.
1974. The mammals of Louisiana and its adjacent waters. Louisiana State Univ. Press, Baton Rouge, LA, 565 p.

Norris, K. S., and T. P. Dohl.
1980. The structure and function of cetacean schools. *In* L. M. Herman (ed.), Cetacean behavior: mechanisms and functions, p. 211–261. Wiley, New York, NY.

Payne, P. M., J. R. Nicolas, L. O'Brien, and K. D. Powers.
1986. The distribution of the humpback whale, *Megaptera novaeangliae*, in Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus*. Fish. Bull. 84:271–277.

Perrin, W. F., E. D. Mitchell, J. G. Mead, D. K. Caldwell, and P. J. H. van Bree.
1981. *Stenella clymene*, a rediscovered tropical dolphin of the Atlantic. J. Mammal. 62:583–598.

Perrin, W. F., E. D. Mitchell, J. G. Mead, D. K. Caldwell, M. C. Caldwell, P. J. H. van Bree, and W. H. Dawbin.
1987. Revision of the spotted dolphins, *Stenella* spp. Mar. Mamm. Sci. 3:99–170.

Rice, D. W.
1989. Sperm whale *Physeter macrocephalus* Linnaeus, 1758. *In* S. H. Ridgway and R. Harrison (eds.), Handbook of marine mammals, Vol. 4: River dolphins and the larger toothed whales, p. 177–234. Academic Press, San Diego, CA.

Ross, G. J. B.
1978. Records of pygmy and dwarf sperm whales, genus *Kogia*, from southern Africa, with biological notes and some comparisons. Ann. Cape Prov. Mus. 11:259–327.

Schmidly, D. J.
1981. Marine mammals of the southeastern United States coast and the Gulf of Mexico. U.S. Fish Wildl. Ser., Office of Biological Service, Washington, D.C. FWS/OBS-80/41, 163 p.

Scott, M. D., and J. G. Cordaro.
1987. Behavioral observations of the dwarf sperm whale, *Kogia simus*. Mar. Mamm. Sci. 3:353–354.

Scott, M. D., and S. J. Chivers.
1990. Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific. *In* S. Leatherwood and R. R. Reeves (eds.), The bottlenose dolphin, p. 387–402. Academic Press, San Diego, CA.

Sekiguchi, K., N. T. W. Klages, and P. B. Best.
1992. Comparative analysis of the diets of smaller ondontocete cetaceans along the coast of southern Africa. S. Afr. J. Mar. Sci. 12:843–861.

Selzer, L., and P. M. Payne.
1988. The distribution of white-sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) vs. environmental features of the continental shelf of the northeastern United States. Mar. Mamm. Sci. 4:141–153.

Townsend, C. H.
1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica 19:3–50.

United States Fish and Wildlife Service (USFWS).
1989. Endangered and threatened wildlife and plants. 50 CFR 17.11 and 17.12, Division of Endangered Species and Habitat Conservation. U.S. Fish Wildl. Ser. Washington, D.C. 20240.

Vidal, O., L. T. Findley, P. J. Turk, and R. E. Boyer.
1987. Recent records of pygmy sperm whales in the Gulf of California. Mar. Mamm. Sci. 3:354–356.

Voss, G. L.
1971. The cephalopod resources of the Caribbean sea and adjacent regions. *In* Symposium on investigations and resources of the Caribbean Sea and adjacent regions, p. 307–323. FAO, Fish. Rep. 71.2.

Voss, G. L., and T. F. Brakoniecki.
1985. Squid resources of the Gulf of Mexico and Southeast Atlantic coasts of the United States. *In* NAFO Scientific Council Studies Number 9, Special session on squids, p. 27–37. September 1984, Dartmouth, Nova Scotia, Canada.

Wade, P. R., and T. Gerrodette.
1993. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. Rep. Int. Whaling Comm. 43:477–493.

Weber, M., R. T. Townsend, and R. Bierce.
1990. Environmental quality in the Gulf of Mexico: a citizen's guide. Center for Marine Conservation, Washington, D.C., 130 p.

Wells, R. S., A. B. Irvine, and M. D. Scott.
1980. The social ecology of inshore odontocetes. *In* L. M. Herman (ed.), Cetacean behavior: mechanisms and functions, p. 263–317. Wiley, New York, NY.

Yamada, M.
1954. Some remarks on the pygmy sperm whale, *Kogia*. Sci. Rep. Whales Res. Inst. 9:37–61.

Abstract.—Reef fish communities at Gray's Reef National Marine Sanctuary, Georgia, differed over five different habitat types. Numbers of species and overall densities were highest on ledge habitat, intermediate on live-bottom (three categories of low relief [<15 cm] rock outcroppings covered by algae and macrofauna), and lowest over sand. On average, abundance over ledges exceeded that over sand bottoms by a factor of 50. Generally, community composition at sites over ledges and dense live-bottom areas was similar and distinct from sites found over sparse live-bottom and sand. Many species were found in more than one habitat and few individual species could be considered indicators of a single habitat type. A nondestructive, repeatable procedure of randomly dispersed video transects was devised for assessing diurnally active fishes.

A video transect method for estimating reef fish abundance, composition, and habitat utilization at Gray's Reef National Marine Sanctuary, Georgia

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The geographic and depth distribution of fishes associated with reefs or hard bottom off the southeastern U.S. coast is generally known (Struhsaker, 1969; Huntsman and Manooch, 1978; Miller and Richards, 1980; Powles and Barans, 1980; Wenner, 1983; Chester et al., 1984; Sedberry and Van Dolah, 1984; Parker and Ross, 1986). Most of these studies have demonstrated changes in community structure associated with different depths and water temperatures. Although trawl collections over sand have been compared with collections over hard bottom (Wenner, 1983; Sedberry and Van Dolah, 1984), no quantitative in situ studies of the distribution of reef fishes by type of substrate have been published.

Gray's Reef National Marine Sanctuary (GRNMS), Georgia, one of 14 Marine Sanctuaries managed by the National Oceanic and Atmospheric Administration (NOAA), encompasses nearly 32 km^2 at a depth of about 22 m. Compared with surrounding areas, Gray's Reef contains extensive, but patchy and discontinuous, hardbottom of moderate relief (up to 2 m). Rock outcrops or "ledges" have formed in a northwest to southeast direction (Fig. 1). Ledges are often separated by wide expanses of sand and are subject to weathering, shifting sand, and slumping, which create a complex habitat with caves, burrows, troughs, and overhangs (Hunt, 1974). Sandy areas between the ledges consist of coarse shell with varying amounts of "rock-like" litter (Henry and Van Sant[1]).

Reef fish assemblages are difficult to sample because of the diversity and mobility of the fauna and because of the variety of microhabitats within complex reef substrates (Russell et al., 1978). The applicability and limitations of various techniques for estimating reef fish abundance have been reviewed (Russell et al., 1978; Sale, 1980; Sale and Douglas, 1981; Brock, 1982; DeMartini and Roberts, 1982; Sale and Sharp, 1983; Kimmel, 1985; Sanderson and Solonsky, 1986; Bortone and Kimmel, 1991).

[1] Henry, V. J., Jr., and S. B. Van Sant. 1982. Results of reconnaissance mapping of the Gray's Reef National Marine Sanctuary, a report prepared for the Georgia Department of Natural Resources, Coastal Resources Division, Brunswick, GA, under cooperative agreement with the Sanctuary Programs Division of the National Oceanic and Atmospheric Administration (No. NA81AA44-C2098, Amendment 1), 21 p.

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Fishery Bulletin 92:787–799.

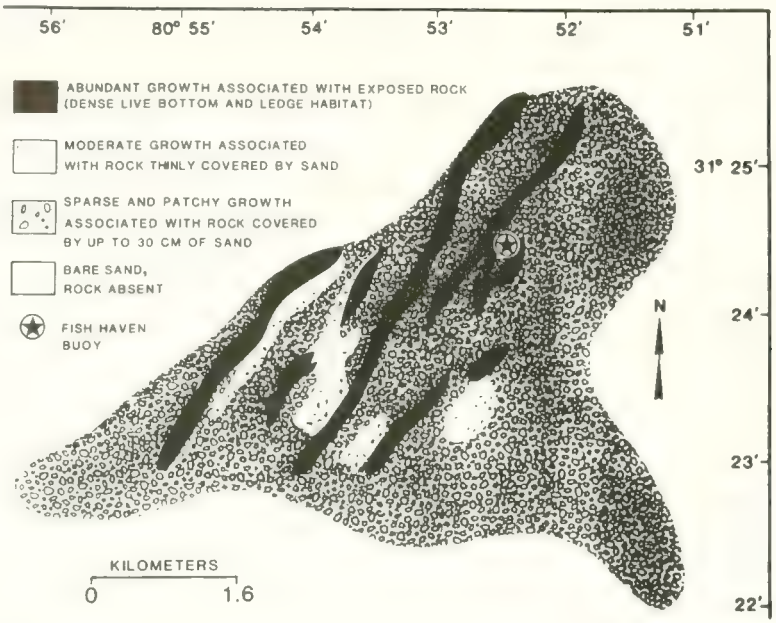

Figure 1

Sand, live-bottom, and ledge substrates at Gray's Reef National Marine Sanctuary (GRNMS) (after Hunt, 1974).

Techniques include the use of traditional fisheries assessment gear (nets, traps, and hook-and-line), poisons, explosives, and visual observations. The need for repeatable surveys and the constraints of working in a national marine sanctuary necessitated the use of nondestructive survey techniques.

Diver observations are the most common method used in studies of reef fish assemblages (Brock, 1954; Bardach, 1959; Hobson, 1972; Chave and Eckert, 1974; Sale, 1975; Jones and Chase, 1975; Jones and Thompson, 1978; Anderson et al., 1981; Ogden and Ebersole, 1981; Sale and Douglas, 1981; Brock, 1982; Kimmel, 1985; Bohnsack and Bannerot, 1986; Parker, 1990). Although a variety of sampling techniques have been employed to make quantitative assessments of reef fish abundance, all rely on divers to identify and record fish species observed in a predefined area (transect and point counts) or over a period of time (rapid visual assessment techniques). Accuracy of the visual techniques is affected by light levels, water clarity, currents, fish species diversity and densities, substrate complexity, diver familiarity with the fishes, and number and size of the sampling units. Biases are induced by 1) a tendency to undersample small, cryptic, and nocturnal species (Brock, 1982); 2) identification, counting, and recording errors (Brock, 1954; Russell et al., 1978); 3) attraction and aversion reactions of some species to the divers (Chapman et al., 1974); and 4) species differences in territory, home range, life history patterns, and behavior (Russell et al., 1978).

Remote observation techniques, using movie or closed-circuit television cameras deployed from vessels or carried by divers, have been used to estimate abundance of reef fish (Smith and Tyler, 1973; Alevizon and Brooks, 1975; Powles and Barans, 1980; Boland et al.[2]). A major advantage is that a permanent record of observed fishes is obtained without destroying the fauna. However, remote systems that are tethered to a surface vessel are severely limited by sea conditions. In addition, camera resolution, light levels, water clarity, depth, and lack of in situ guidance limit the effectiveness of remote observations, and biases are imposed by the attraction or avoidance of some species to the gear.

The objectives of this study were 1) to develop a nondestructive, repeatable procedure for assessing diurnally active fishes inhabiting Gray's Reef National Marine Sanctuary, and 2) to describe and compare fish communities associated with ledge, live-bottom, and sand habitats.

[2] Boland, G., B. Galloway, J. Baker, and G. S. Lewbel. 1984. Ecological effects of energy development on reef fish of the Flower Garden Banks. Final Rep. Contract No. Na80-GA-C-00057. U.S. Natl. Mar. Fish. Serv., Galveston, TX, 466 p.

Methods

Research site selection

Based on preliminary observations (1–2 May 1985), 30,000 m^2 of bottom in GRNMS were divided empirically into sand, live-bottom, and ledge habitats (Parker et al.[3]). For detailed community analyses, the live-bottom area was further divided into three subunits. The habitat classifications and approximate proportional areas within GRNMS (calculated from Hunt, 1974) were the following:

Sand: sand or sand and shell bottom with bottom relief (<20 cm) provided by sandy swales; occasional (<1%) depressions or burrows (5–25 cm deep) in sand surrounded by algae, macrofauna, and sometimes rocks; approximately 18% of GRNMS.

Live-bottom: approximately 1 to 75% of bottom composed of rock outcroppings covered by algal and benthic macrofauna; little or no (<15 cm) relief; sandy areas, 2 to 25 cm deep,underlaid by rock; approximately 58% of GRNMS.

a Sparse live-bottom: covers 1 to 25% of the substrate.

b Moderate live-bottom: covers 26 to 50% of the substrate.

c Dense live-bottom: covers greater than 50% of the substrate.

Ledge: distinct rock outcroppings of 15 cm to over 200 cm; associated rock bottoms covered by algal and benthic macrofauna; approximately 24% of GRNMS.

Thirty-six potential sampling sites, 12 each over sand, live-bottom, and ledge substrates, were randomly selected from a pool of 76 locations of known habitat type defined by our preliminary work and by existing Georgia Department of Natural Resources data (Nicholson[4]; Hudson[5]). Of the 36 sites, 14, 17, 9, and 12, respectively, were randomly selected for sampling during four surveys: summer (15–22 August) and fall (13–18 November) 1985, and spring (13–18 May) and summer (21–27 August) 1986. Sampling was stratified by habitat type.

As a stratified random design, optimal allocation of effort among habitats normally would be determined by the variance of the population size of a particular species and the size of each habitat. For this study we used species richness as a proxy for variance because the focus was on a multispecies assemblage. Although the relationship between species richness and total variance is not clearly defined, even approximate estimators of variance usually are adequate for allocating sampling effort (Steel and Torrie, 1960).

Because the sample size of our preliminary work on live-bottom habitat was roughly one-third the number of intervals available for sand and ledge habitats (Fig. 2), we extrapolated the live-bottom data (10 species observed in eight sampling intervals) to a hypothetical sample of 25 sampling intervals. On both ledge and sand habitats approximately 71% of the total species observed were encountered after eight sampling intervals (Fig. 2). Assuming the same relationship for live-bottom data, 14 species would have been encountered in 25 sampling intervals. Prior experience by both diving investigators suggests this is a reasonable approximation. Sampling effort was allocated among the different reef habitats in proportion to the product of the area of a given

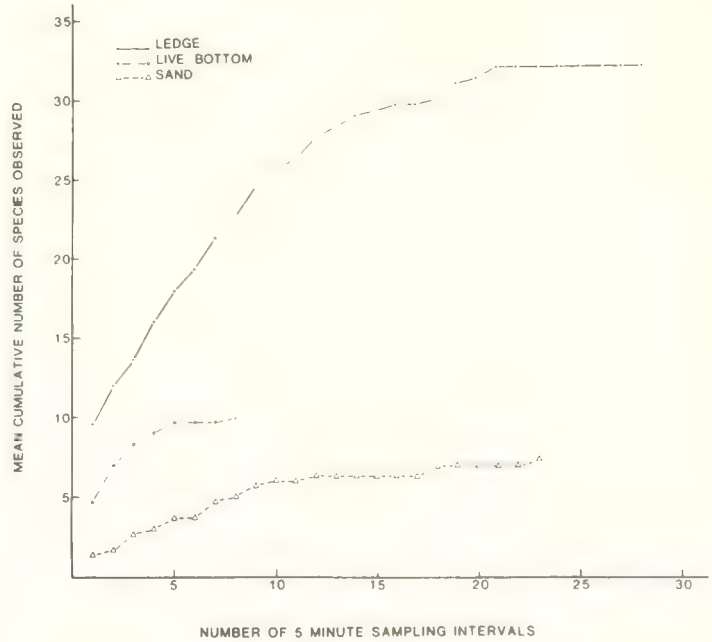

Figure 2
Species vs. time curve from preliminary work, May 1985.

[3] Parker, R. O., Jr., R. S. Nelson, and A. J. Chester. 1988. A quantitative approach to the estimation of reef fish abundance and community composition in the Gray's Reef National Marine Sanctuary using SCUBA divers. Final Rep. Contract No. NA84DOC-C2004. U.S. Natl. Ocean Serv., Washington, D.C., 71 p.

[4] Nicholson, N. 1982. The Gray's Reef National Marine Sanctuary Visual Reef Fish Censusing Workshop, final report. Georgia Dep. Nat. Resour., Coastal Resour. Div., Brunswick, 16 p.

[5] Hudson, J. A. 1984. Summer Internship Report, Valdosta State College, Georgia Dep. Nat. Resour., Coastal Resour. Div., Brunswick, 33 p.

habitat times the square root of anticipated species richness for that habitat (adapted from Steel and Torrie, 1960).

The preliminary data (Fig. 2) indicate that 19, 5-minute sampling intervals (95 minutes) were sufficient to observe at least 95% of the total species recorded in each habitat during the preliminary work. A maximum of 40 dives, limited to 20 minutes of survey time per dive (four 5-minute intervals), were available for each of the four surveys. Thus, the available sampling time likely was sufficient to obtain a complete record of the noncryptic species present in each habitat.

Sampling procedures

All dives were completed between 0930 and 1630 hours to take advantage of maximum light levels. At each site a marker buoy was deployed at the start of a transect. One of three dive teams, each consisting of two divers, swam a 15-minute transect with the prevailing current. One diver operated a color video camera with a 51-mm lens; the other towed a surface buoy. The video operator waved his hand in front of the camera to signify the beginning and end of each transect. Appearance of the towed buoy released by divers signaled to the boat the beginning of a transect. The camera was held in a rigid forward position about 1 m off the bottom. Fishes in cryptic locations were not recorded by the video camera. At the termination of a transect the camera was turned off, the towed surface buoy was anchored, a standard black and white Secchi disk (30 cm in diameter) was used to measure horizontal visibility, and bottom water temperature was recorded.

During each transect swim the vessel approached the towed buoy at 5-minute intervals, and the crew recorded the LORAN C coordinates and plotted its position. The plots were used to measure the length of each transect and to calculate distance covered during each 5-minute interval. Transect length and Secchi disk visibility could be used to estimate area sampled. However, after reviewing the initial tapes, we estimated the transect width to be 4 m (2 m on each side of focal center), because small fishes (70 to 150 mm) could be identified with certainty only out to an estimated distance of 2 m. Larger fish were recorded as they came into view. To avoid duplicate counts, only maximum numbers of species that passed by the camera more than once were used. These species were easily identified by the camera operator. Because transect width remained constant, data are reported as number of fish per meter of transect. Generally, two transects were swum at each site, beginning at the same location and heading with the prevailing current. Plots of the transects showed little overlap.

Videotaped transects were viewed to estimate abundance of each species seen within each 5-minute interval. Videotapes were projected on a 50-cm color NEC Corporation Television and were analyzed by a single observer. Viewing was in real time with frequent pauses, reverses, and repeated counts until the observer obtained the same count of species three times. Date, location, Secchi disk measurement, bottom water temperature, and number of each species per type of habitat were recorded on data sheets. Because habitat type often changed during a transect, habitat changes were closely monitored and species were apportioned appropriately.

Community analysis

Species-specific data were summarized by habitat type. Statistical analysis, data summarization, and graphic representation were accomplished with SAS version 6.03 software system (SAS, 1987). Data were summarized over sites within habitats and surveys, and the effects of survey (4 surveys) and habitat (3 habitat types) on total fish density and number of species observed were tested with two-way ANOVA's.

Cluster analysis was used to classify Gray's Reef sampling sites according to the species composition of the fish community. Species that were not found in at least 10% of ledge, live-bottom, or sand sites in any one survey were eliminated. For each survey, relative abundance data (number/m of transect) were arranged in a species-by-site matrix, standardized by dividing each element by the square root of the product of the row total and column total (simultaneous double standardization), and converted to a site-by-site Canberra Metric dissimilarity matrix (Clifford and Stephenson, 1975). Sites were grouped by means of the "flexible sorting" algorithm of Lance and Williams (1967) and the cluster intensity coefficient was set at –0.25 to approximate the median clustering strategy. Analysis was conducted with SIMCLUST statistical software (Wolfe and Chester, 1991).

Results

A total of 110 transects covering a distance of 24 km (4.9 km over ledge, 12.7 km over live-bottom, and 6.4 km over sand) were made during the study. Over 92,000 fish, including 66 species and 36 families, were recorded and identified from the videotapes (Table 1).

Number of species and density of fish (individuals/m transect) varied significantly among the four surveys

Table 1

Species observed at Gray's Reef National Marine Sanctuary (GRNMS) between 12 August 1985 and 27 August 1986 in ledge (L), live-bottom (LB), sand (S), or pelagic (P) habitats. Species indicated by asterisk in column labeled 'Both sites' represent those seen in study site off North Carolina by Parker (1990) and those seen at GRNMS, whereas those species indicated in GRNMS column represent those seen only at GRNMS.

	Habitat					
Species	L	LB	S	P	Both sites	GRNMS
Orectolobidae						
Ginglymostoma cirratum, nurse shark	*				*	
Dasyatidae						
Dasyatis americana, southern stingray	*		*		*	
Muraenidae						
Moray, unidentified	*					
Ophichthidae						
Myrophis punctatus, speckled worm eel		*	*			*
Clupeidae						
Brevoortia tyrannus, Atlantic menhaden			*	*		*
Sardinella aurita, Spanish sardine	*	*	*	*	*	
Synodontidae						
Synodus foetens, inshore lizardfish		*	*			*
Trachinocephalus myops, snakefish	*	*				*
Batrachoididae						
Opsanus sp., toadfish[1]	*	*	*			*
Holocentridae						
Holocentrus ascencionis, squirrelfish	*	*				*
Syngnathidae						
Hippocampus erectus, lined seahorse		*	*			*
Micrognathus crinitus, banded pipefish		*				*
Syngnathus louisianae, chain pipefish			*			*
Serranidae						
Centropristis ocyurus, bank sea bass	*	*			*	
C. philadelphica, rock sea bass	*	*				*
C. striata, black sea bass	*	*	*		*	
Diplectrum formosum, sand perch	*	*	*		*	
Mycteroperca microlepis, gag	*	*			*	
M. phenax, scamp	*	*			*	
Serranus subligarius, belted sandfish	*	*			*	
Grammistidae						
Rypticus maculatus, whitespotted soapfish	*	*			*	
Priacanthidae						
Priacanthus arenatus, bigeye	*	*				
Pristigenys alta, short bigeye		*				*
Apogonidae						
Apogon pseudomaculatus, twospot cardinalfish	*	*			*	
Phaeoptyx pigmentaria, dusky cardinalfish		*				*

Continued on next page

Table 1 (Continued)

Species	Habitat					
	L	LB	S	P	Both sites	GRNMS
Carangidae						
Caranx bartholomaei, yellow jack	*	*		*		*
C. ruber, bar jack	*	*		*	*	
Caranx sp., unidentified jack	*			*		
Decapterus punctatus, round scad	*	*	*	*	*	
Seriola dumerili, greater amberjack	*	*		*	*	
S. rivoliana, almaco jack	*			*	*	
Lutjanidae						
Lutjanus campechanus, red snapper	*	*			*	
Lutjanus sp., juvenile snapper		*				
Haemulidae						
Haemulon aurolineatum, tomtate	*	*			*	
Orthopristis chrysoptera, pigfish	*					*
Sparidae						
Archosargus probatocephalus, sheepshead	*	*			*	
Calamus leucosteus, whitebone porgy	*	*			*	
Diplodus holbrooki, spottail pinfish	*	*			*	
Pagrus pagrus, red porgy	*	*			*	
Stenotomus caprinus, longspine porgy	*	*	*		*	
Sciaenidae						
Equetus acuminatus, high-hat	*	*				*
E. lanceolatus, jacknife-fish	*	*			*	
E. umbrosus, cubbyu	*	*			*	
Mullidae						
Mullus auratus, red goatfish	*					*
Ephippidae						
Chaetodipterus faber, Atlantic spadefish	*	*		*	*	
Chaetodontidae						
Chaetodon ocellatus, spotfin butterflyfish	*				*	
C. sedentarius, reef butterflyfish	*	*			*	
C. striatus, banded butterflyfish	*	*			*	
Pomacanthidae						
Holocanthus bermudensis, blue angelfish	*				*	
Pomacentridae						
Pomacentrus partitus, bicolor damselfish	*	*			*	
P. variabilis, cocoa damselfish	*	*			*	
Sphyraenidae						
Sphyraena barracuda, great barracuda	*	*		*	*	
Labridae						
Halichoeres bivittatus, slippery dick	*	*	*		*	
Hemipteronotus novacula, pearly razorfish	*	*	*			*
Tautoga onitis, tautog	*		*		*	

Continued on next page

Table 1 (Continued)

Species	Habitat					
	L	LB	S	P	Both sites	GRNMS
Scaridae						
Sparisoma sp., parrotfish	*					*
Opistognathidae						
Unidentified jawfish		*	*			
Blenniidae						
Ophioblennius atlanticus, redlip blenny	*	*				*
Parablennius marmoreus, seaweed blenny	*				*	
Unidentified	*	*				
Gobiidae						
Ioglossus calliurus, blue goby	*	*			*	
Microgobius carri, Seminole goby	*	*	*			*
Acanthuridae						
Acanthurus bahianus, ocean surgeon	*	*			*	
A. chirurgus, doctorfish	*	*			*	
Scombridae						
Euthynnus alleteratus, little tunny		*		*	*	
Scomberomorus maculatus, Spanish mackerel		*	*	*		*
Stromateidae						
Psenes maculatus, silver driftfish		*				*
Triglidae						
Prionotus sp., unidentified searobin		*	*			*
Bothidae						
Unidentified flounder		*				*
Balistidae						
Aluterus heudoloti, dotterel filefish	*	*				*
A. schoepfi, orange filefish	*	*				*
Balistes capriscus, gray triggerfish	*	*			*	
Monocanthus hispidus, planehead filefish	*	*			*	
Ostraciidae						
Lactophrys quadricornis, scrawled cowfish	*	*				*
L. triqueter, smooth trunkfish	*					*
Diodontidae						
Diodon hystrix, porcupinefish			*		*	
Others						
fish	*	*	*	*		
larval fish	*			*		
juvenile fish	*	*	*	*		
Number of taxa	63	62	22	15	42	28

[1] *Opsanus* sp. is likely an undescribed offshore form.

and three major habitat types (two-way ANOVA, $P<0.05$, no significant survey × habitat interaction). Numbers of species and overall densities were greatest on ledge habitats, intermediate on live-bottom, and smallest over sand (Figs. 3 and 4, Table 2). Numbers of species and densities were highest during the summer of 1985, intermediate during the fall of 1985 and summer of 1986, and lowest during the spring of 1986 (Table 2). The lower number of species observed in spring of 1986 may be a result of fewer samples having been taken because of inclement weather. Underwater visibility varied from 2.4 to 17.9

m but did not affect identification and counts, since it exceeded 2 m (see Methods section).

Species composition differed over five different habitat types (Table 3). Nearly three times as many species were identified from ledge habitats (63) than from sand habitats (22), and over one-third as many species were seen on ledge as were seen on either dense (46) or moderate (46) live-bottom. More species were recorded over dense and moderate live-bottom than over sparse live-bottom (33). Mean relative abundances also were related to habitat; highest values were found for ledge habitat, progressively declining values for the three live-bottom habitats, and lowest values for sand. On average, abundances over ledges exceeded those over sand bottoms by a factor of 50.

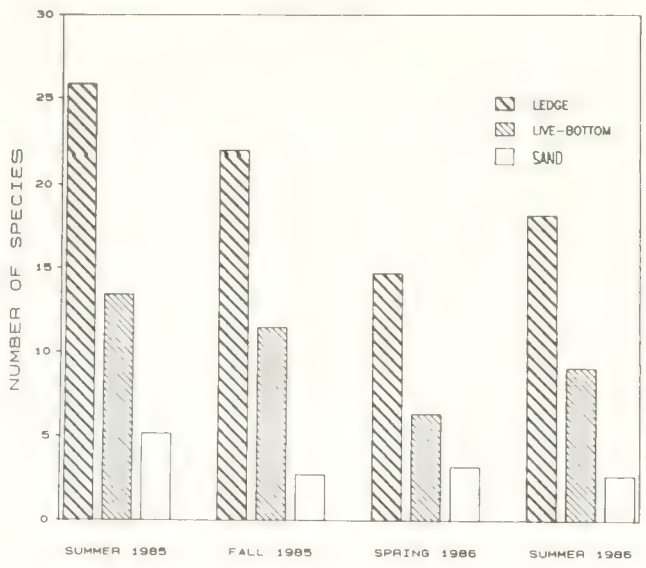

Figure 3

Number of species observed at Gray's Reef National Marine Sanctuary by survey and habitat.

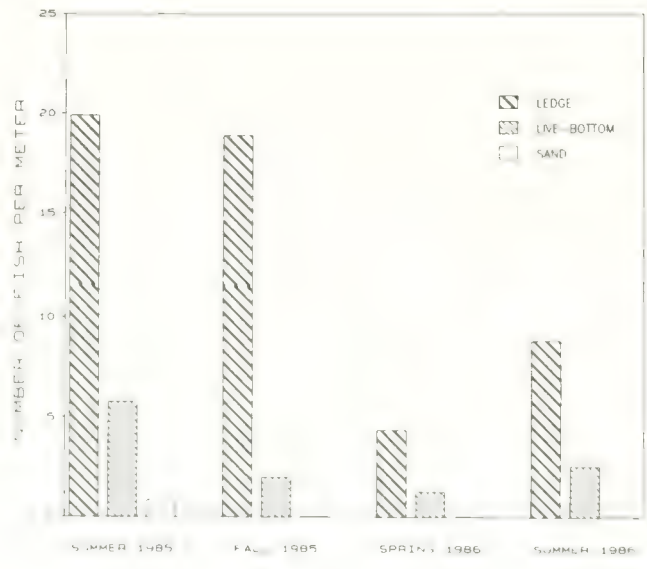

Figure 4

Density of fish (estimated means) at Gray's Reef National Marine Sanctuary by survey and habitat. Number of fish/m over sand for fall 1985, spring 1986, and summer 1986 was 0.02.

Cluster analyses for each of the four surveys (Fig. 5) indicate clear distinctions in community composition among habitats. Generally, sites over ledges and dense live-bottom areas were classified similarly and were distinct from sites found over sparse live-bottom and sand. Classification of moderate live-bottom sites was more variable. Many species were present in more than one habitat (Tables 1 and 3), and few individual species could be considered indicators of a single habitat type. The following species were present at more than half the respective habitat sites. Ledges were characterized by black sea bass,[6] belted sandfish, gag, scamp, sand perch, round scad, tomtate, sheepshead, spottail pinfish, longspine porgy, cubbyu, Atlantic spadefish, slippery dick, doctorfish, and planehead filefish. Dense live-bottom was characterized by black sea bass, belted sandfish, tomtate, longspine porgy, and slippery dick. Moderate live-bottom had black sea bass, belted sandfish, round scad, longspine porgy, and slippery dick. Sparse live-bottom had black sea bass, round scad, longspine porgy, and slippery dick. Sand habitats were relatively depauperate but were best characterized by the presence of pearly razorfish.

Discussion

Comparison of the fauna of GRNMS with that of other reefs off the southeastern U.S. coast suggests a high level of variability among reef communities. The fish species composition at GRNMS differs considerably from that of an intensely studied reef in 30 m of water, 44 km south of Beaufort Inlet, North Carolina (Parker, 1990). Of 113 species observed by divers at the two reefs, only 42 (37%) were common to both (Table 1). Twenty-eight species were unique to GRNMS (Table 1) and 43 species were seen only at the North Carolina site. Although more effort was expended at GRNMS

[6] Scientific names of fishes in this study are listed in Table 1.

(97 transects over 21 hours vs. 51 point counts over 17 hours), 15 more species were observed off North Carolina. The major difference appears to be that more temperate species usually associated with inshore environments (i.e. inshore lizardfish, toadfish, rock sea bass, pigfish, pearly razorfish, and Spanish mackerel) were present at GRNMS, whereas more tropical species (i.e. red grouper, harlequin bass, wrasse bass, white grunt, knobbed porgy, and queen angelfish) were seen at the North Carolina location. The warm waters of the Gulf Stream provide a mechanism for recruitment and survival of many tropical species (Briggs, 1974). GRNMS is 12 km closer to shore and 8 m shallower than the North Carolina site. More importantly, although the position of the Gulf Stream varies across the continental shelf, it generally follows the 200-m isobath which is much farther offshore from GRNMS (105 km) than from the North Carolina site (40 km).

The diversity of species collected is partly a reflection of the sampling method. Our observations on species abundance agree only partially with results obtained by trawling. The 10 most abundant and common species observed in this study (Table 3) included four (tomtate, black sea bass, cubbyu, and longspine porgy) of the most abundant species caught by trawling over hardbottom similar to GRNMS off the southeastern U.S. coast (Wenner, 1983; Sedberry and Van Dolah, 1984; Table 4). Size, form, and behavior of three of the other six species may preclude their capture by trawls. Two of the three most abundant species (round scad and slippery dick) are small and fusiform and can pass through the meshes of most trawls. Slippery dick and belted sandfish usually live close to the bottom where they are protected from trawls by the substrate. Round scad have been seen swimming freely in and out of the mouth of trawls towed up to 3.5 knots (Workman[7]). A major source of unmeasured error in many visual assessments is observer error in sighting, identifying, counting, and recording. In a prior study of ledge fishes at GRNMS, 10 divers operating in pairs per-

[7] Workman, I. NOAA, NMFS, Mississippi Laboratory, Pascagoula, MS 39567. Personal commun., January 1994.

Table 2

Mean number of species and density (number/m), standard errors, and number of site-habitat combinations (n) for each cruise at Gray's Reef National Marine Sanctuary, Georgia.

			Species		Density	
Cruise	Habitat	n	Mean	SE	Mean	SE
1	Ledge	6	25.83	2.40	19.90	4.09
	Live-bottom	12	13.42	1.47	5.77	1.51
	Sand	6	5.17	1.01	0.85	0.49
2	Ledge	7	21.86	2.54	18.87	7.54
	Live-bottom	13	11.46	1.37	2.00	0.77
	Sand	7	2.71	0.57	0.02	0.01
3	Ledge	3	14.67	0.33	4.35	2.12
	Live-bottom	6	6.33	0.95	1.26	1.09
	Sand	5	3.20	1.20	0.02	0.01
4	Ledge	6	18.17	1.66	8.82	2.82
	Live-bottom	11	9.09	0.94	2.57	0.96
	Sand	3	2.67	0.33	0.02	0.01

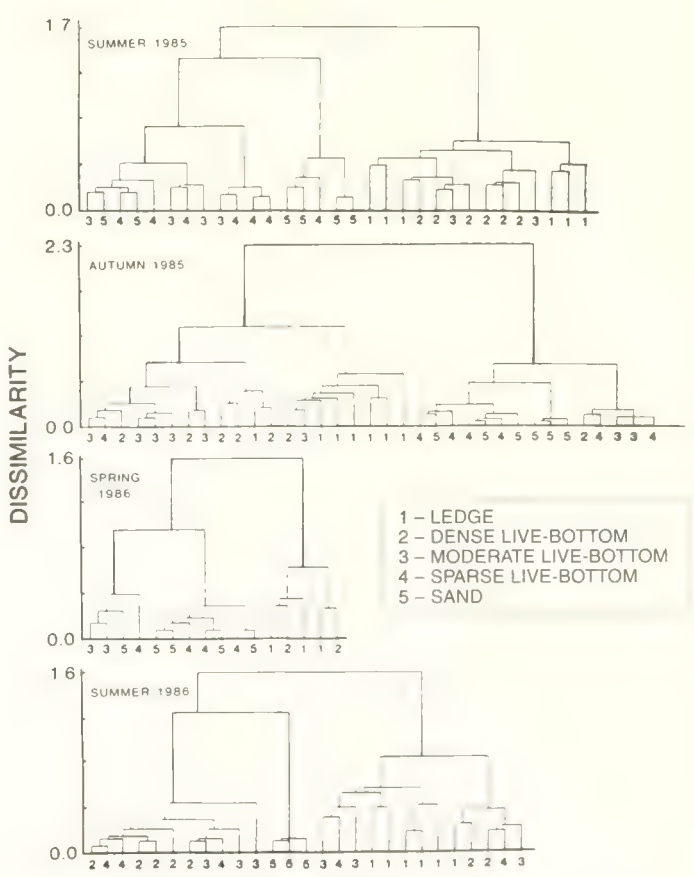

Figure 5

Dendrograms of cluster analyses of sites referenced by habitat type for each of four surveys conducted in Gray's Reef National Marine Sanctuary. Note that dissimilarity axes differ in scale.

Table 3

Numbers of fish per meter transect and number[1] of sites present (in parentheses) by habitat at Gray's Reef National Marine Sanctuary, August 1985–August 1986.

Species	Ledge (*n*=22)	Dense live-bottom (*n*=22)	Moderate live-bottom (*n*=22)	Sparse live-bottom (*n*=23)	Sand (*n*=21)
Centropristis striata	0.52 (22)	0.28 (20)	0.08 (22)	0.01 (16)	0.00 (4)
C. ocyurus	0.01 (3)	0.01 (5)	0.01 (6)	0.00 (8)	
C. philadelphica	0.00 (7)	0.00 (2)	0.00 (5)	0.00 (2)	
Serranus subligarius	0.22 (22)	0.13 (21)	0.03 (14)	0.00 (6)	
Mycteroperca microlepis	0.04 (17)	0.04 (5)	0.00 (3)		
M. phenax	0.02 (15)	0.00 (3)	0.00 (1)		
Diplectrum formosum	0.00 (15)	0.01 (8)	0.01 (11)	0.01 (11)	0.00 (7)
Rypticus maculatus	0.02 (11)	0.00 (2)	0.00 (1)		
Decapterus punctatus	3.41 (15)	2.62 (11)	2.24 (13)	0.46 (12)	0.09 (8)
Seriola dumerili	0.14 (10)	0.02 (4)	0.00 (2)	0.01 (4)	
Caranx bartholomaei	0.05 (6)	0.00 (1)	0.00 (1)	0.00 (2)	
Haemulon aurolineatum	5.95 (21)	0.88 (12)	0.28 (7)	0.00 (1)	
Archosargus probatocephalus	0.02 (12)	0.00 (2)	0.00 (3)		
Calamus leucosteus	0.00 (5)	0.00 (2)	0.00 (2)		
Diplodus holbrooki	0.17 (20)	0.02 (8)	0.02 (4)		
Pagrus pagrus	0.00 (3)		0.00 (1)		
Stenotomus caprinus	0.13 (20)	0.48 (15)	0.57 (19)	0.43 (16)	0.15 (5)
Equetus acuminatus	0.02 (7)	0.01 (2)	0.00 (2)	0.00 (1)	
E. lanceolatus	0.01 (11)	0.01 (3)	0.00 (4)	0.00 (1)	
E. umbrosus	0.49 (22)	0.06 (7)	0.05 (3)	0.02 (1)	
Chaetodipterus faber	0.09 (12)	0.00 (1)			
Chaetodon sedentarius	0.02 (7)	0.00 (2)	0.00 (4)		
C. ocellatus	0.00 (3)				
Holocanthus bermudensis	0.01 (7)				
Pomacentrus variabilis	0.03 (11)	0.01 (3)			
Halichoeres bivittatus	1.72 (22)	1.18 (22)	0.38 (22)	0.10 (19)	0.00 (1)
Hemipteronotus novacula	0.00 (1)	0.00 (2)	0.00 (1)	0.00 (8)	0.01 (14)
Sphyraena barracuda	0.01 (8)	0.01 (5)			
Ioglossus calliurus	0.01 (4)	0.00 (5)	0.00 (4)	0.00 (1)	
Sparisoma sp.	0.00 (4)				
Ophioblennius atlanticus	0.01 (5)	0.00 (1)	0.00 (1)		
Microgobius carri	0.00 (1)	0.00 (1)	0.00 (3)	0.00 (5)	0.00 (4)
Acanthurus chirurgus	0.04 (13)	0.02 (10)	0.00 (2)		
A. bahianus	0.02 (9)	0.00 (1)	0.00 (1)		
Balistes capriscus	0.00 (5)	0.00 (1)	0.00 (1)		
Monacanthus hispidus	0.01 (16)	0.00 (4)	0.00 (6)	0.00 (1)	
Lactophrys quadricornis	0.00 (4)	0.00 (1)		0.00 (1)	
Lutjanus campechanus	0.00 (4)			0.00 (2)	
Synodus foetens		0.00 (1)	0.00 (3)	0.00 (1)	0.00 (2)
Opsanus sp.	0.00 (4)	0.00 (3)	0.00 (7)	0.00 (7)	0.00 (2)
Holocentrus ascencionis	0.00 (3)	0.00 (1)	0.00 (1)		
Syngnathus louisianae					0.00 (3)
Apogon pseudomaculatus	0.01 (8)	0.00 (4)			
Unidentified blenny	0.00 (3)	0.00 (1)	0.00 (1)		
Priacanthus arenatus	0.00 (1)	0.00 (2)	0.00 (3)	0.00 (3)	
Ginglymostoma cirratum	0.00 (3)				
Caranx ruber	0.02 (6)		0.00 (1)		
Number of taxa[2]	63	46	46	33	22
Mean density per site	14.43	5.84	3.72	1.25	0.26

[1] The total number of live-bottom sites is greater in this table than in Table 4 because the subdivision of live-bottom habitat into three categories yielded more site-habitat combinations.

[2] From Table 1.

Table 4

Ten most abundant and common hardbottom species observed by divers or caught by trawl.

Ranking	Divers[1]	Trawls A[2]	Trawls B[3]
1	*Haemulon aurolineatum*	*Stenotomus caprinus*	*Stenotomus caprinus*
2	*Decapterus punctatus*	*Haemulon aurolineatum*	*Haemulon aurolineatum*
3	*Halichoeres bivittatus*	*Chromis enchrysurus*	*Rhomboplites aurorubens*
4	*Centropristis striata*	*Monacanthus hispidus*	*Equetus lanceolatus*
5	*Equetus umbrosus*	*Centropristis striata*	*Centropristis striata*
6	*Serranus subligarius*	*Rhomboplites aurorubens*	*Prionotus carolinus*
7	*Diplodus holbrooki*	*Calamus leucosteus*	*Calamus leucosteus*
8	*Seriola dumerili*	*Holocanthus bermudensis*	*Equetus umbrosus*
9	*Stenotomus caprinus*	*Equetus umbrosus*	*Urophycis regia*
10	*Chaetodipterus faber*	*Apogon psuedomaculatus*	*Monocanthus hispidus*

[1] This study, 22 m deep.
[2] Wenner, 1983; < 18–183 m deep, day and night catches combined.
[3] Sedberry and Van Dolah, 1984; 16–67 m deep.

formed five counts of species and individuals (Nicholson[4]). Although all divers were experienced in underwater surveys and were familiar with the fauna, the mean percent similarity for the five teams was only 57% and ranged from 47% to 64%. Videotaping reduces the variance in error among observers and allows virtually unlimited time for study of the images by many individuals (Ebeling et al., 1980).

In choosing between transect and point sampling, we considered the particular conditions at GRNMS. When properly applied, the precision of both procedures can be high (Keast and Harker, 1976; Sale and Douglas, 1981; DeMartini and Roberts, 1982; Bohnsack and Bannerot, 1986; Witzig, 1988). Limited visibility at GRNMS was thought to bias point counts for some species. Bohnsack and Bannerot (1986) found that point samples with a radius of 2 m or less underestimated abundances of 11 of 15 species observed. In contrast, Parker (1990) found that during low visibility some species of reef fish (e.g. gag, black sea bass, and white grunt) concentrate under and around ledges. Extrapolating density of these fish in a small visible area to the total population over an entire reef that consists mostly of low profile (<1 m) rock outcroppings sparsely inhabited by fishes grossly overestimates their abundance. Off-bottom tidal currents, frequently in excess of 20 cm/s at GRNMS, make it impossible for the vessel to remain stationary for the 5 to 10 minutes necessary to conduct enumerations. For these reasons we developed a random transect technique that allowed us to swim with the prevailing current, covering 86 to 544 m per transect. Because visibilities at GRNMS can be consistently less than 5 m, this technique allowed us to sample large areas with minimum underwater time. The technique is a consistent, repeatable procedure for assessing the noncryptic, diurnally active fishes at GRNMS.

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Literature cited

Alevizon, W. S., and M. G. Brooks.
1975. The comparative structure of two western Atlantic reef fish assemblages. Bull. Mar. Sci. 25:482–490.

Anderson, G. R. V., A. H. Ehrlich, P. R. Ehrlich, J. D. Roughgarden, B. C. Russell, and F. H. Talbot.
1981. The community structure of coral reef fishes. Am. Nat. 117:476–495.

Bardach, J. E.
1959. The summer standing crop of fish on a shallow Bermuda reef. Limnol. Oceanogr. 4:77–85.

Bohnsack, J. A., and S. P. Bannerot.
1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. Dep. Commer., NOAA Tech. Rep. NMFS 41, 15 p.

Bortone, S. A., and J. J. Kimmel.
1991. Environmental assessment and monitoring of artificial habitats. *In* W. Seaman Jr. and L. M. Sprague (eds.), Artificial habitat for marine and freshwater fisheries, p. 177–236. Academic Press, New York.

Briggs, John C.
1974. Marine zoogeography. McGraw-Hill, New York, 475 p.

Brock, R. E.
1982. A critique of the visual census method for assessing coral reef fish populations. Bull. Mar. Sci. 32:269–276.

Brock, V. F.
1954. A preliminary report on a method of estimating reef fish populations. J. Wildl. Manage. 18:299–308.

Chapman, C., A. Johnstone, J. Dunn, and D. Creasey.
1974. Reactions of fish to sound generated by diver's open-circuit underwater breathing apparatus. Mar. Biol. 27:357–366.

Chave, E. H., and D. B. Eckert.
1974. Ecological aspects of the distribution of fishes at Fanning Island. Pac. Sci. 28:297–317.

Chester, A. J., G. R. Huntsman, P. A. Tester, and C. S. Manooch III.
1984. South Atlantic Bight reef fish communities as presented in hook-and-line catches. Bull. Mar. Sci. 34:267–279.

Clifford, H. T., and W. Stephenson.
1975. An introduction to numerical classification. Academic Press, New York, 229 p.

DeMartini, E. E., and D. Roberts.
1982. An empirical test of biases in the rapid visual technique for species-time censuses of reef fish assemblages. Mar. Biol. 70:129–134.

Ebeling, A. W., R. J. Larson, W. S. Alevizon, and R. N. Bray.
1980. Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California. Fish. Bull. 78:361–377.

Hobson, E. S.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull. 70:715–740.

Hunt, J. L., Jr.
1974. The geology and origin of Gray's Reef, Georgia continental shelf. M.S. thesis, Univ. Georgia, Athens, 83 p.

Huntsman, G. R., and C. S. Manooch III.
1978. Coastal pelagic and reef fishes in the South Atlantic Bight. *In* H. Clepper (ed.), Marine recreational fisheries, Vol. 3, p. 97–106. Sport Fish. Inst., Washington, D.C.

Jones, R. S., and J. A. Chase.
1975. Community structure and distribution of fishes in an enclosed high island lagoon in Guam. Micronesia 11:127–148.

Jones, R. S., and M. J. Thompson.
1978. Comparison of Florida reef fish assemblages using a rapid visual survey technique. Bull. Mar. Sci. 28:159–172.

Keast, A., and J. Harker.
1976. Strip counts as a means of determining densities and habitat utilization patterns in lake fishes. Environ. Biol. Fishes 1:181–189.

Kimmel, J.
1985. A new species-time method for visual assessment of fishes and its comparison with established methods. Environ. Biol. Fishes 12:23–32.

Lance, G. N., and W. T. Williams.
1967. A general theory of classificatory sorting strategies. I: Hierarchical systems. Comput. J. 9:373–380.

Miller, G. C., and W. J. Richards.
1980. Reef fish habitat, faunal assemblages, and factors determining distributions in the South Atlantic Bight. Proc. Gulf Caribb. Fish. Inst. 32:114–130.

Ogden, J. C., and J. P. Ebersole.
1981. Scale and community structure of coral reef fishes: a long term study of a large tropical artificial reef. Mar. Ecol. Prog. Ser. 4:97–103.

Parker, R. O., Jr.
1990. Tagging studies and diver observations of fish populations on live-bottom reefs of the U.S. southeastern coast. Bull. Mar. Sci. 46:749–760.

Parker, R. O., Jr., and S. W. Ross.
1986. Observing reef fishes from submersibles off North Carolina. Northeast Gulf Sci. 8:31–49.

Powles, H., and C. Barans.
1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. Mar. Fish. Rev. 42(5):21–35.

Russell, B. C., F. H. Talbot, G. R. V. Anderson, and B. Goldman.
1978. Collection and sampling of reef fishes. *In* D. R. Stoddart and R. E. Johannes (eds.), Coral reefs: research methods, p. 329–345. UNESCO, Paris.

Sale, P. F.
1975. Patterns of use in a guild of territorial reef fishes. Mar. Biol. 29:89–97.
1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Annu. Rev. 18:367–421.

Sale, P. F., and W. A. Douglas.
1981. Precision and accuracy of visual census technique for fishes assemblages on coral patch reefs. Environ. Biol. Fishes 6:333–339.

Sale, P. F., and B. J. Sharp.
1983. Correction for bias in visual transect censuses of coral reef fishes. Coral Reefs 2:37–42.

Sanderson, S. L., and A. C. Solonsky.
1986. Comparison of a rapid visual and a strip transect technique for censusing reef fish assemblages. Bull. Mar. Sci. 39:119–129.

SAS (SAS Institute, Inc.).
1987. Changes and enhancements to base SAS. Software for personal computers, release 6.03. SAS Tech. Rep. Cary, NC, 171 p.

Sedberry, G. R., and R. F. Van Dolah.
1984. Demersal fish assemblages associated with hard bottom habitat in the South Atlantic Bight of the U.S.A. Environ. Biol. Fishes 11:241–258.

Smith, C. L., and J. C. Tyler.
1973. Population ecology of a Bahamian suprabenthic shore fish assemblage. Am. Mus. Novit. 2528, 38 p.

Steel, R. G. D., and J. H. Torrie.
1960. Principles and procedures of statistics. McGraw-Hill, New York, 581 p.

Struhsaker, P.
1969. Demersal fish resources: composition, distribution, and commercial potential of the continental shelf stocks off southeastern United States. Fish. Ind. Res. 4:261–300.

Wenner, C. A.
1983. Species associations and day-night variability of trawl-caught fishes from the inshore sponge-coral habitat, South Atlantic Bight. Fish. Bull. 81:537–552.

Witzig, J. F.
1988. Visual assessment of reeffish communities. Ph.D. thesis, NC State Univ., Raleigh, 161 p.

Wolfe, N. A., and A. J. Chester.
1991. SUMCLUST: a cluster analysis program for ecological data. Am. Stat. 45:158.

Abstract. —Approximately 12,396 Pacific cod, *Gadus macrocephalus*, were tagged and released from fishery research vessels in the eastern Bering Sea and adjacent waters between 1982 and 1990. Recapture data from 373 tags recovered through the first quarter of 1992 revealed a strong seasonal component in fish movement between summer and winter areas. Prespawning fish were tagged throughout their summer distribution, primarily over the inner and middle shelf (<30–100 m depths), and recaptured on the outer shelf (>100–200 m) and upper continental slope (>200 m) in subsequent quarters. Recoveries from the winter quarter (January–March) showed the most directed movement, when Pacific cod aggregated in major spawning areas between Unalaska and Unimak islands in the eastern Aleutian Islands, seaward of the Pribilof Islands along the shelf edge in the eastern Bering Sea, and near the Shumagin Islands in the western Gulf of Alaska. By early summer, a hypothesized postspawning dispersal was observed from these overwintering areas, when tagged Pacific cod moved from deep off-shelf waters to shallower depths on the eastern Bering Sea shelf. The importance of seasonal migration was examined statistically by contingency table analysis, which indicated that season of recovery affected area of recovery more than either the season or area of tagging. Seasonal movements were further quantified by modeling the population dynamics of tagged individuals, which allowed estimation of the seasonal distribution in the eastern Bering Sea population. These estimated seasonal distributions compare well with the seasonal distribution of catches from the commercial fisheries. This analysis of tag-recapture data suggests a single winter spawning population in the eastern Bering Sea, nearby waters of the Aleutian Islands, and western Gulf of Alaska waters between longitude 157°W and 170°.W

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Seasonal movements of Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea and adjacent waters based on tag-recapture data

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Pacific cod, *Gadus macrocephalus*, are widely distributed throughout the North Pacific Ocean. Off North America, Pacific cod range from California north through British Columbia and southeast Alaska, into the Bering Sea, and west along the Aleutian Islands (Bakkala et al., 1984). Pacific cod are found epibenthically over the Bering Sea shelf and slope. The Bering Sea represents the center of greatest regional abundance, although Pacific cod are also abundant in the neighboring Aleutian Islands and Gulf of Alaska waters (OCSEAP, 1987). Pacific cod catches rank third among the eastern Bering Sea groundfish resources following walleye pollock, *Theragra chalcogramma*, and yellowfin sole, *Pleuronectes asper* (Low, 1991).

Beginning in the early 1980's, Pacific cod catches increased substantially above the 10,000 to 50,000 metric tons (t) landed annually between 1958 and 1979. Eastern Bering Sea and Aleutian Islands catches over the last decade have averaged 132,500 t; a historic high of 198,000 t was taken in 1988 (Thompson, 1994). Much of this growth was due to the recruitment of exceptionally strong 1977–78 year classes, in combination with greater fishing effort from joint-venture (i.e. U.S. fishing vessels delivering catches to foreign processors at sea) and new domestic groundfish fisheries (Bakkala, 1984; Shimada, 1985). More recently, the eastern Bering Sea and Aleutian Islands Pacific cod fishery generated a catch of 177,300 t, valued at $90 million in 1991 (NMFS, 1992). These developments in resource availability and in expanding fishery exploitation patterns provided the impetus for new studies into the biology of Pacific cod in Alaskan waters.

In September 1982, a pilot tagging experiment for Pacific cod and walleye pollock in the eastern Bering Sea was conducted by National Marine Fisheries Service (NMFS) scientists from the Alaska Fisheries Science Center (AFSC). The initial objective of this experi-

ment was to evaluate the feasibility of a tag-recapture program for Pacific cod and walleye pollock (Shimada[1]). During the second year, as tag-recovery information accumulated, field efforts focused exclusively on Pacific cod because few tagged walleye pollock were recovered. Growth-increment data obtained from these tag returns have been analyzed by Kimura et al. (1993). This paper presents new information on the seasonal movements and long-range migration of Pacific cod in the eastern Bering Sea and adjacent waters.

Materials and methods

Between 1982 and 1990, Pacific cod were successfully captured and released from AFSC-chartered fishing vessels engaged in summer bottom trawl surveys off Alaska. Pacific cod were tagged throughout their eastern Bering Sea distribution (Fig. 1). This effort was augmented by tag releases from cooperating Japanese, Korean, and U.S. research vessels operating in the Aleutian Islands and Gulf of Alaska (Fig. 1).

Capture gear included bottom trawls, pots, and hook-and-line. For the bottom trawl, predetermined stations were sampled each year across the eastern Bering Sea shelf (Bakkala, 1993). Thirty-minute trawl hauls and biological samplings were performed at each station. Occasional opportunistic hauls of 10 to 30-minute durations were made to obtain additional tag releases. On retrieval of the trawl net, Pacific cod were taken from the unprocessed portion of the catch and placed in on-deck holding tanks supplied with running sea water. After a recovery period (typically 1–2 h), fish were removed with a dip net and examined for visible signs of injury or stress. Those not seriously harmed during capture were placed in a padded cradle, tagged, and measured for fork length to the nearest 0.5 cm. General condition was noted, and fish were quickly returned to the sea.

Two tag types were used in this study: 3.5-inch anchor tags and 8-inch lock-on spaghetti tags.[2] Both types were constructed from international orange #20 vinyl tubing and labeled with a tag serial number and return address. The majority of releases were made with the spaghetti tag (69%). This tag was applied through the dorsal musculature, behind the head and anterior to the first dorsal fin, with a hollow needle applicator and secured by interlocking plastic terminals. Anchor tags were inserted between individual fin rays at the base of the first or second dorsal fin.

Pacific cod were tagged across the entire size range available to the capture gears (Fig. 2); priority was placed on the release of fish less than 55 cm (i.e. younger than about age 5 yr; conversion from length to age in this paper is based on growth data in Kimura and Lyons [1990]). Pacific cod smaller than about 42 cm (i.e. age 3 yr or younger) were not recruited to the commercial fisheries and were of particular interest as the preexploited population component; however, owing to availability larger fish made up the majority of tagged fish. Data recorded at release included date, haul or set number, gear type, depth fished, bottom water temperature, release position, fork length, and general fish health.

Tag information from Pacific cod recovered by commercial trawl, longline, and pot fisheries (Table 1) through the first quarter of 1992 were used in this paper. The Bering Sea groundfish fishery was dominated by foreign fishing until 1987, when harvest allocations shifted to joint-venture and domestic fisheries. By early 1991, the Pacific cod fishery had evolved into an exclusively U.S. enterprise. Mirroring this transition in fleet involvement, tag recoveries initially came from foreign and joint-venture trawl and foreign longline fisheries. More recent tag returns have come from the domestic trawl and longline fisheries. Tag recovery reports provided information regarding capture date, catch location, and body length. Some tag returns also included capture method, depth fished, sex, body weight, maturity, and a collection of scales or otoliths.

Tag recovery data were analyzed by three complementary methods: 1) mapping, which described the location of release or recovery or the movement of fish from the area of tagging to the area of recovery; 2) multiway contingency table analysis (Fienberg, 1977), which was used to analyze the strength of relationships between the season and area of tagging and the season and area of recovery; and 3) direct population dynamics modeling of the tagged population.

Three primary areas of interest (Fig. 3) were defined for use in the mapping, contingency table analysis, and the population dynamics model: 1) the inner shelf from depths <30 m to 100 m [Area 1]; 2) the outer shelf between >100 m and 200 m and incorporating the upper continental slope at depths greater than 200 m [Area 2]; and 3) winter spawning grounds surrounding Unimak Pass and adjacent waters [Area 3].

To emphasize the main features in the data, release-recovery positions were plotted individually (Fig. 4) and as mean-movement vectors based on tags released over blocks of 2° latitude × 5° longitude (Fig.

[1] Shimada, A. M. 1982. Cruise results, NOAA ship *Chapman*, Cruise CH-82-06, 7 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., Bin C15700, Seattle, WA 98115-0070.

[2] Floy FD68BC anchor tag and FT-4C lock-on spaghetti tag.

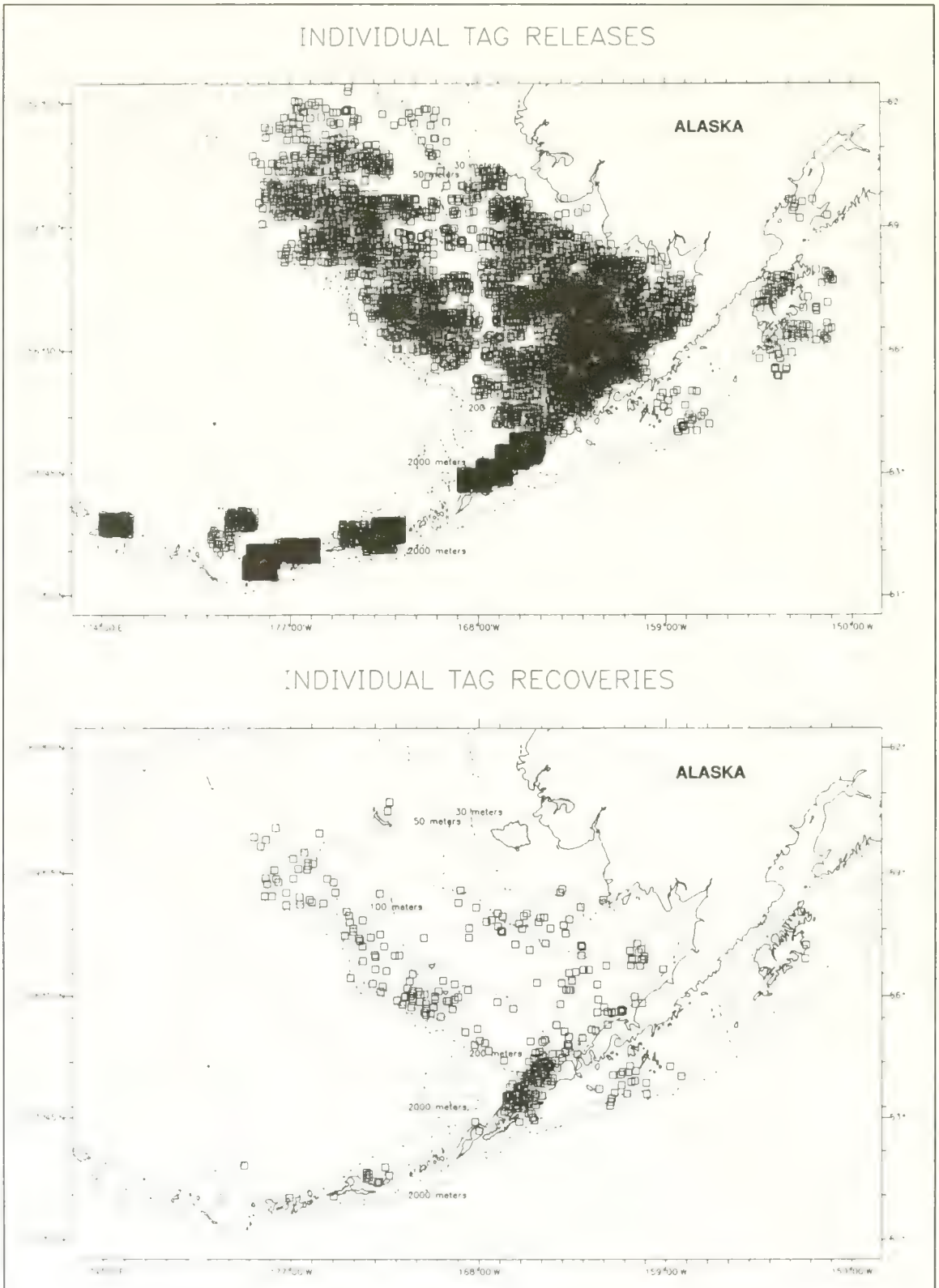

Figure 1

Jittered plots showing locations of individual Pacific cod, *Gadus macrocephalus*, tag releases (R=12,396) and recoveries (r=373), 1982–92. "Jittering" is accomplished by adding small amounts of random noise to the data to avoid overplotting.

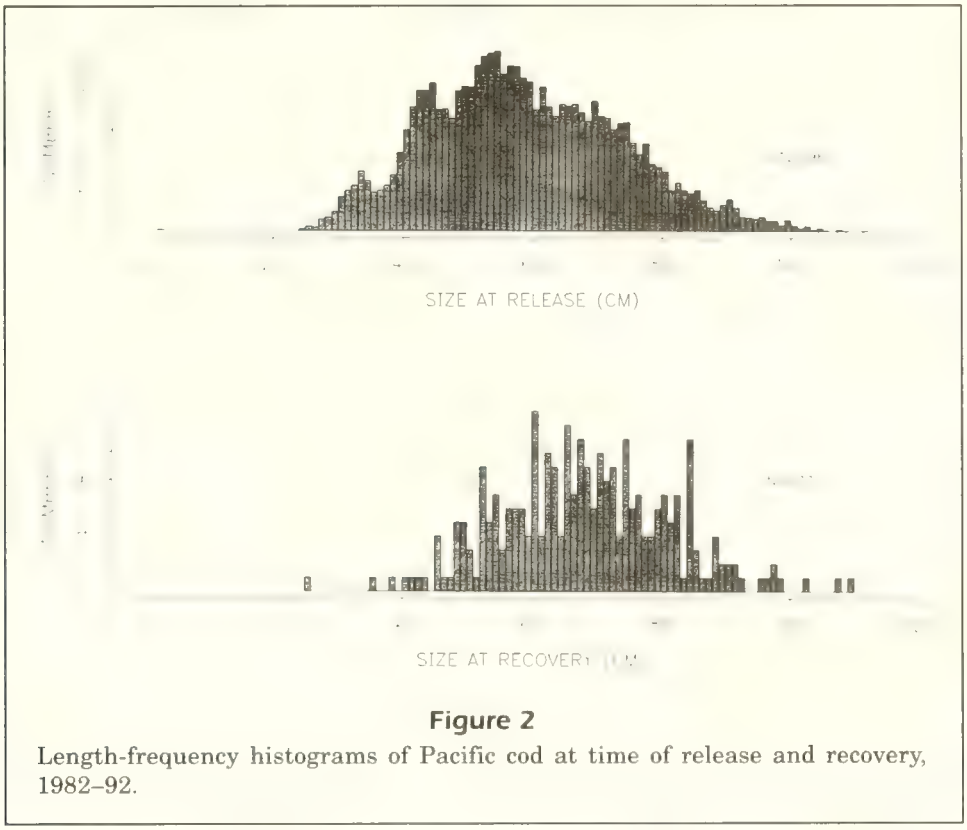

Figure 2

Length-frequency histograms of Pacific cod at time of release and recovery, 1982–92.

5) and aggregated by recovery season (winter=Jan–Mar, spring=Apr–Jun, summer=Jul–Sept, and fall=Oct–Dec; this definition of seasons is used throughout the paper). For these plots each $2^{\circ} \times 5^{\circ}$ block is associated with just one arrow.

The modeling of the tagged population was performed similarly to that done by Hilborn (1990) and by Heifetz and Fujioka (1991). However, rather than describing movement through time as a Markov process, we only estimated seasonal distribution, a much easier task. Our model assumed that the quarterly natural mortality rate (M) was the same in all seasons and areas, and that the instantaneous fishing mortality rate (F) varied by season but not by area. Years were assumed to be homogeneous (i.e. we assumed no year effects). Modeling the tagged population allowed the estimation of seasonal distribution by taking into account the actual time and area of tagging and recovery.

The model assumed that time (i) is divided into seasons (four per year over all years, so that the subscript i runs from 1 to 4 × nyr, where nyr=10, the number of years being modeled) and that there are three areas (j) being modeled.

Table 1

Tabulations of tag releases and tag recoveries (top) by areas described in Figure 3 (Area 1=the eastern Bering Sea shelf, Area 2=the outer eastern Bering Sea shelf and upper slope, Area 3= the main spawning area) for Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea. Percentage release and recoveries by fishing gear (bottom).

	Release		Recovery	
Area	Number	Percent	Number	Percent
1	4,967	40.1	91	24.4
2	1,303	10.5	107	28.7
3	3,048	24.6	158	42.4
Other	3,078	24.8	17	4.5
Total	12,396		373	

Release		Recovery	
Gear	Percent	Gear	Percent
Trawl	97.2	trawl	62
Hook and line	0.6	longline	24
Pot	2.2	pot	2
Unknown	0.0	unknown	12

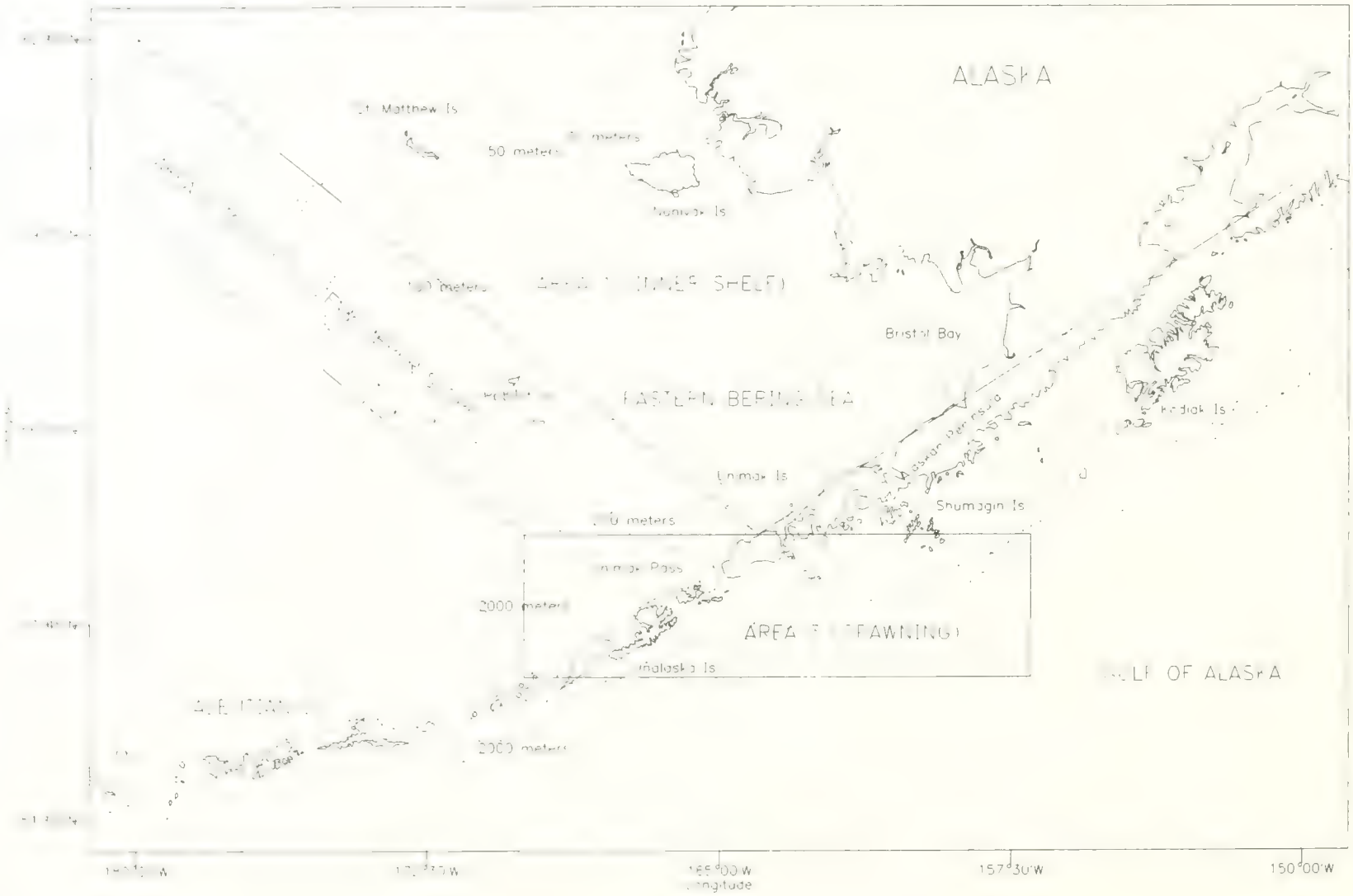

Figure 3

Map of the eastern Bering Sea showing the regional bathymetry and area boundaries (3 areas) used for mapping, contingency table analysis, and population dynamics modeling.

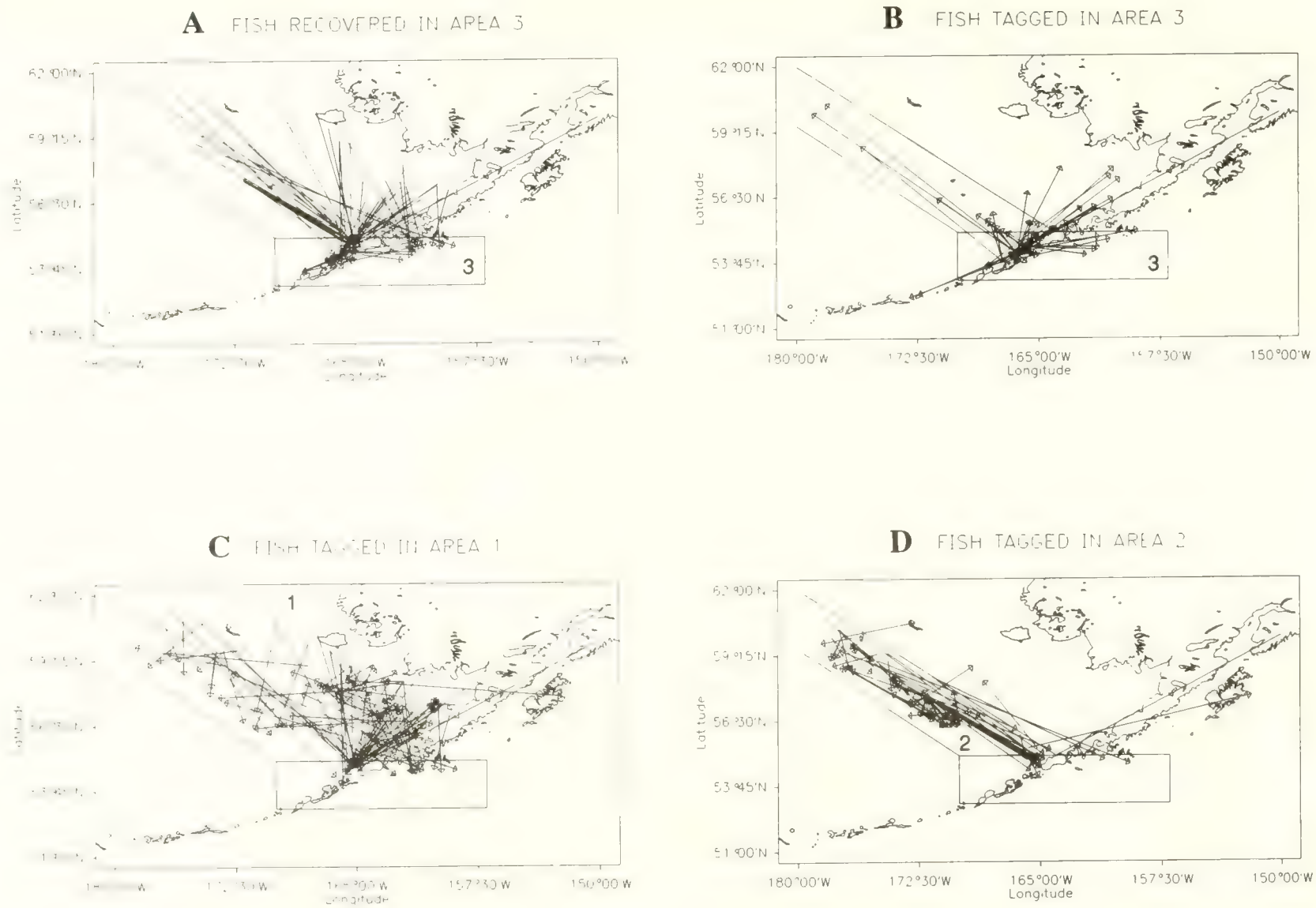

Figure 4

(**A**) Movement of individual Pacific cod recovered in the spawning area (Area 3); (**B**) movement of individual Pacific cod tagged in the spawning area (Area 3); (**C**) movement of individual Pacific cod tagged in the inner shelf (Area 1); (**D**) movement of individual Pacific cod tagged in the outer shelf and slope (Area 2).

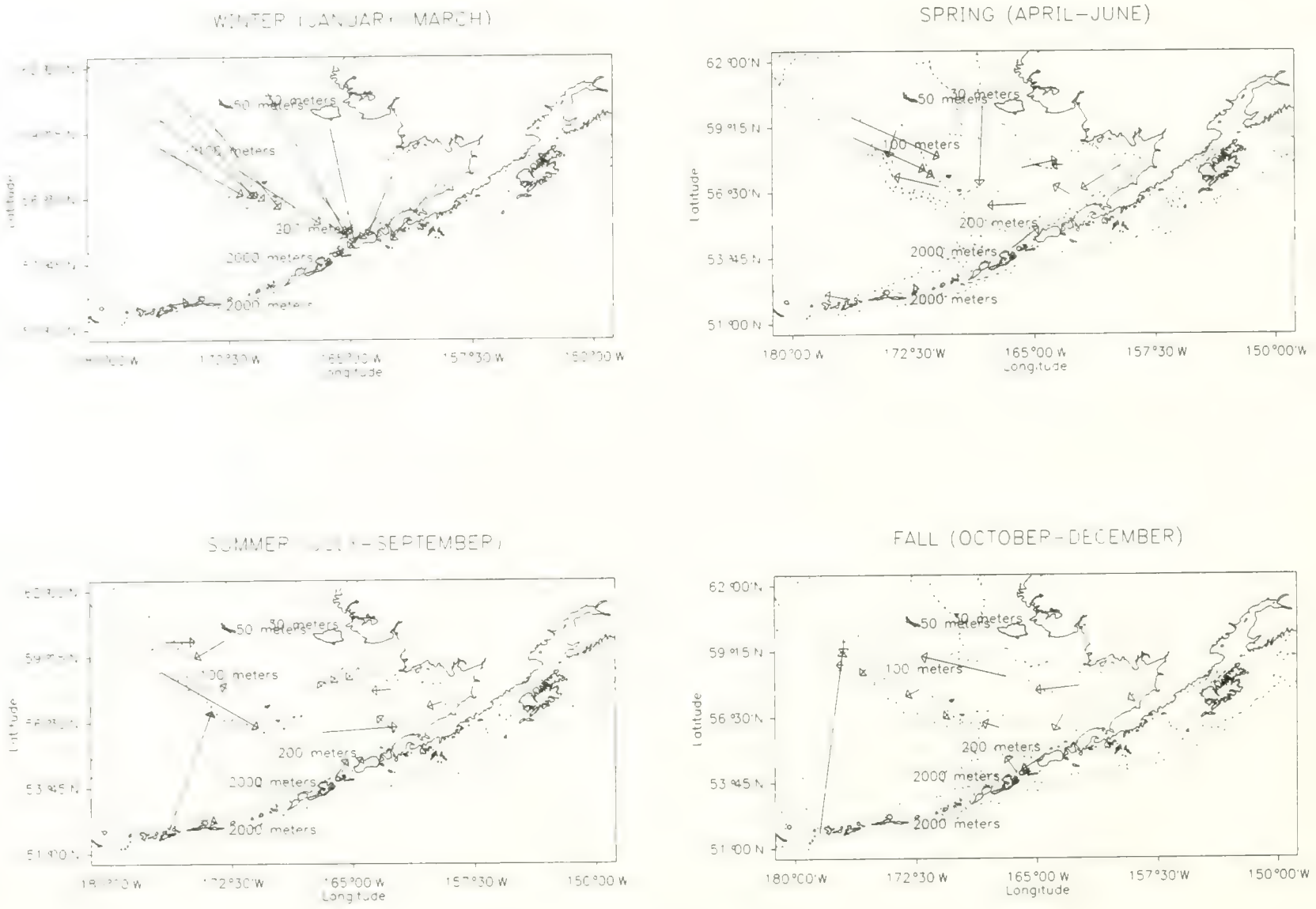

Figure 5

Average seasonal movement of Pacific cod from release to recapture locations. Average movement calculated from all tags released from 2° latitude × 5° longitude reporting blocks and recovered during a specific season.

Let

R_{ij} = the number of fish tagged in time period i in area j,

r_{ij} = the recoveries of tagged fish in time period i in area j,

N_{ij}^{b} = the number of tags at the beginning of time period i in area j, *after* tags have been redistributed according to estimates of their seasonal distribution,

N_{ij}^{e} = the number of tags at the end of time period i in area j,

s_{ij} = $s_i = \exp(-M - F_{s(i)})$ the survival of tagged fish in time period i and area j,

u_{ij} = $u_i = F_{s(i)}\left(1.0 - \exp(-M - F_{s(i)})\right)/(M + F_{s(i)})$ the exploitation rate of tagged fish in time period i and area j, and

$p_{s(i)}$ = the areal distribution by seasonal time period.

Here, the subscript $s(i)$ refers to the season corresponding to the time period subscript i. Therefore $s(i)$ could be w=winter, sp=spring, su=summer, or f=fall. Each seasonal area-distribution vector (p_w for example) is a vector containing one element for each of the three areas.

There are 13 parameters to be estimated in this model: the seasonal distribution vectors (p_w, p_{sp}, p_{su}, p_f); the seasonal instantaneous rates of fishing mortality (F_w, F_{sp}, F_{su}, F_f); and the seasonal instantaneous natural mortality rate (M). The seasonal area-distribution vectors each contain only two parameters to be estimated because they are probability distributions that must sum to one. The model is tied together by three simple equations:

$$\hat{N}_{ij}^{e} = \hat{N}_{ij}^{b}\hat{s}_i + R_{ij}\sqrt{\hat{s}_i},$$

$$\hat{r}_{ij} = \hat{N}_{ij}^{b}\hat{u}_i + R_{ij}\hat{u}_i/2,$$

$$\hat{N}_{i+1,j}^{b} = \left(\sum_j \hat{N}_{ij}^{e}\right)\hat{p}_{j[s(i+1)]}.$$

Here, $\hat{p}_{j[s(i+1)]}$ represents the estimated proportion of tags in area j in season s (i+1). Note that $\sqrt{\hat{s}_i}$ and $\hat{u}_i/2$ are the estimated survival and exploitation rates, respectively, over half a season.

Following Hilborn (1990) and Heifetz and Fujioka (1991), the model was fit by using maximum likelihood and by assuming recoveries were distributed as Poisson random variables. That is, the parameters were estimated by minimizing minus the log-likelihood:

$$-L = \sum_{ij} \hat{r}_{ij} - r_{ij}\log(\hat{r}_{ij}) + const.$$

The probabilities in (p_w, p_{sp}, p_{su}, p_f) were modeled as expressions similar to exploitation rates following the method of Heifetz and Fujioka (1991). Parameters were estimated on the logarithmic scale and coefficients of variation were estimated by using the inverse Hessian of the minus log-likelihood and the delta method.

Our seasonal population dynamics model of the tagged population was applied to the areas described in Figure 3. For modeling purposes, we used only fish tagged and recovered in these three areas. Thus, 9,318 releases,

$$\left(\sum_{ij} R_{ij}\right),$$

and 353 recoveries,

$$\left(\sum_{ij} r_{ij}\right),$$

were available for analysis.

A problem associated with our population dynamics model is the strong assumption that the $F_{s(i)}$ are constant across areas. An attempt was made to use existing commercial trawl and longline data to determine recovery effort, but these data varied too much in their seasonal coverage, and gears and areas were confounded.

Nevertheless, the population dynamics model provides evidence that our tag data are representative of the entire eastern Bering Sea population. In the following sections we present evidence that our tagging study probably suffered from significant tag loss, tag mortality, or under-reporting of tag recoveries. By comparing the estimated seasonal distribution of the tagged population with the distribution from commercial catches, we can verify that the tagged population and untagged population were distributed similarly. Since catch distribution should reflect abundance in a heavily fished region such as the eastern Bering Sea, we interpret this as meaning that the behavior of the tagged Pacific cod population largely reflected similar patterns in the entire Bering Sea population. Commercial catch statistics were taken from the Alaska and Pacific Northwest Historical Groundfish Database (Berger[3]), from which we calculated the areal trawl and longline catch distribution (for numbers), by season, for the 1982–92 study period.

Results

Approximately 12,396 tagged fish were released between 1982 and 1990 (Table 1; Fig. 1). A total of 373

[3] Berger, J. Alaska Fish. Sci. Cent., Seattle, WA 98115-0070. Personal commun., January 1993.

tag recaptures with useful information were reported to the AFSC through March 1992 for a recovery rate of 3.0%. Although tag returns occurred over a broad area and time period, this rate is much lower than the 24–26% recovery rate reported by Canadian and U.S. researchers working off British Columbia, Canada, and in Puget Sound, Washington (Westrheim, 1984; Karp, 1982). In our study, research trawl-caught fish accounted for the majority of tag releases (97%), and commercially fished bottom trawls and longlines accounted for the majority of tag recoveries (Table 1). Thompson (1994) estimated that the exploitation rate for Pacific cod in the eastern Bering Sea during 1981–1992 averaged 9–11% annually. This suggests additional tag loss, tagging mortality, or under-reporting of rates which sum to about 2/3 in some combination.

Fish lengths at release were between 25 and 118 cm, representing fish as young as age 2 yr as well as very large, mature fish. The distribution of lengths at recovery corresponds well with the overall tag-release size frequency but is shifted to the right due to growth and gear selectivity (Fig. 2).

In the commercial fisheries, Pacific cod are first recruited at about 40 cm or age 3 yr. They become available to different gear types (i.e. initially to bottom trawls, then to longline gear) at progressively older ages and larger mean size (Shimada, 1985). Most tag recaptures were of commercially recruited, sexually mature fish, older than age 5 yr, and larger than about 60 cm, as defined by Teshima (1985).

More than 75% of all tag releases were from U.S. survey vessels in the eastern Bering Sea (Table 1; Fig. 1). Cooperative foreign research vessels operating in the Aleutian Islands and Gulf of Alaska were responsible for the remaining 25%. Twenty-four percent of recoveries were made over the inner shelf, and 29% over the outer shelf and upper slope (Table 1; Fig. 1). Of particular note was the high concentration of tag recoveries (>42%) in Unimak Pass and its surrounding waters (including the adjacent western Gulf of Alaska) during the winter months (Fig. 1). Only 17 tags (<5%) were recovered from outside the three primary study areas (i.e. from the outer Aleutian Islands and the central Gulf of Alaska).

Mapping seasonal movements

Tagged Pacific cod exhibited marked spatial and temporal displacement from their point of initial release (Fig. 4). Individual movements generally conformed to seasonal shifts in centers of Pacific cod abundance (Ketchen, 1961; Bakkala, 1984) and to the corresponding movement of fishing effort (Shimada, 1985). We attribute the observed pattern in tagged fish movements to hypothesized migratory shifts between perennial summer (feeding) and winter (spawning) areas (Moiseev, 1952, 1953; Ketchen, 1961). This is most easily seen in the vector movements of individual fish into and out of the main spawning area, Area 3. These data were grouped in two ways to show 1) the origin of fish released in all areas and recovered within Area 3 [Fig. 4A]; and 2) the outward recoveries of fish tagged within Area 3 [Fig. 4B]. Although the movement into and out of Area 3 is clear, the movement into the spawning areas seems to occur in two stages: 1) movement off the inner shelf [Area 1] into slope areas [Area 2] [Fig. 4C]; and 2) subsequent movement into spawning areas in Areas 2 and 3 [Fig. 4D]. This shift is counterbalanced by spring and summer recaptures on the inner shelf [Fig. 4B].

The annual cycle of Pacific cod migration appears to begin in late September, when tagged fish move off the eastern Bering Sea shelf and seaward to the 200 m shelf break. By fall, tags were recovered, primarily along the outer shelf edge. In winter, Pacific cod converged in large spawning masses over relatively small areas. Major aggregations were usually encountered between Unalaska and Unimak islands on the Bering Sea side of Unimak Pass. Other recurring centers of abundance were located southwest of the Pribilof Islands along the shelf edge and near the Shumagin Island group in the western Gulf of Alaska (Fig. 1).

Following the spawning season, tagged Pacific cod dispersed from these overwintering areas and were recaptured farther inshore in concert with seasonal warming of the inner shelf environment. For example, fish tagged in areas of deep off-shelf waters adjoining Unimak Pass, close to the time of winter spawning, were recaptured progressively over the shelf (and especially north of the Alaska Peninsula following the 30-m isobath) beginning in late spring. Tagged Pacific cod also moved to the northwest outer shelf (100–200 m) during the spring quarter. By summer, the feeding range was well established back in central Bristol Bay (30–50 m) and the outer shelf. This distribution persisted until late fall and the beginning of the next yearly cycle.

The seasonal nature of Pacific cod movement is most easily seen in the average vector movement of fish tagged within a particular 2° latitude and 5° longitude rectangle and recovered during a specific season (Fig. 5). From these maps, the off-shelf movement is clearly visible in fall, and movement to the spawning ground is clearly visible in winter. However, spring and summer maps show relatively little directed movement, because during these time peri-

ods, Pacific cod have presumably returned to the feeding grounds on which they were originally tagged. The absence of any definitive within-season pattern is further illustrated in Figure 6. Pacific cod released and recaptured during the same three-month period (i.e. within the same season, perhaps in different years) showed only random movement and little directional bearing. This is in marked contrast to the strong interseasonal movements traced between fall-winter and winter-spring quarter tag recaptures.

Multiway contingency analysis

Results from a multiway contingency table analysis (Table 2) indicated that month of recovery most strongly influenced the area of recovery. Although area of tagging also had a significant affect on the area of recovery, the month of tagging was seen to have only a relatively small affect on the area of recovery. Thus season of recovery appeared as the strongest correlate to area of recovery, which further supports our finding of strong seasonal migrations in Pacific cod.

Seasonal-areal population dynamics modeling and catch distribution

A histogram of residuals from predicted tag recoveries indicates that the 13-parameter population dynamics model of the tagged population fit the data quite well (Fig. 7). The parameter estimates from the tagging model (Table 3) show strong movement from the major spawning area (Area 3) in spring, further movement onto the shelf (Area 1) in summer, movement off the shelf in fall, and movement to the spawning areas in winter. Furthermore, the model results confirm strong seasonal movement between areas in a manner consistent with our previously described pattern of seasonal Pacific cod movements.

The apparent high annual instantaneous natural mortality rate ($\hat{M} = 0.96$) and low annual fishing mortality rate ($\hat{F} = 0.038$) of the tagged population can be noted. This is probably due to tag loss, tagging mortality, or the under-reporting of tag recoveries as previously discussed. Multiplying releases by 1/3, or multiplying recoveries by 3 would lower M and increase F nearer to expected levels ($\hat{M} = 0.87, \hat{F} = 0.11$). However, the model fit and estimated seasonal distribution of the tagged population were not affected by this scaling of observed releases or recoveries. Therefore, the population dynamics model estimates of seasonal distribution appear to be robust to tag loss, tag mortality, or under-reporting of recoveries.

The estimated areal distributions (within seasons) of the tagged population largely reflect the areal distribution of tag recoveries. Also, although no catch data were used in the population dynamics model, the results coincide well with the estimated seasonal distribution of the commercial catches (Table 4). The main difference appears to be that the hypothesized fall season off-shelf movement, and subsequent movement into the winter spawning area (Fig. 4, C and D), is more pronounced in the commercial catch data

Table 2

Multiway contingency table analysis of tag recovery data for Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea. The model examined all two-factor interactions (i.e. no factor deletions). Each two-factor interaction was tested for significance by deleting it from the model. Factor 1 = season of release (4 levels), 2 = area of release (3 levels), 3 = season of recovery (4 levels), 4 = area of recovery (3 levels).

Factor deleted	Likelihood ratio stat.	df	P	Test of interaction
none	66.150	96	0.0087	not applicable
[12]	139.382	102	0.9917	(Z=8.786)[1]
[13]	75.892	105	0.0145	(Z=0.291)
[14]	79.206	102	0.0459	(Z=1.793)
[23]	118.317	102	0.8713	(Z=6.898)
[24]	209.201	100	1.0000	(Z=14.269)***
[34]	245.890	102	1.0000	(Z=15.643)***

[1] Interaction large but fixed by design. Z-statistic is a standard normalization of the hierarchical chi-square test.
*** Interactions were significant; α=0.0001.

Table 3

Estimates of parameters (and coefficients of variation measured as proportions) for the population dynamics model for tagged Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea. Areas are shown in Figure 3.

1 Quarterly instantaneous natural mortality rate:

$\hat{M} = 0.235$ (0.109).

2 Seasonal instantaneous fishing mortality rates:

$\hat{F}_w = 0.01389$ (0.149), $\hat{F}_{sp} = 0.0082$ (0.176),
$\hat{F}_{su} = 0.0075$ (0.152), $\hat{F}_f = 0.0087$ (0.141)

3 Seasonal distribution over (Area 1, Area 2, Area 3):

a $\hat{p}_w$ = [0.0246 (0.570), 0.1884 (0.188), 0.7870 (0.047)]
b $\hat{p}_{sp}$ = [0.4849 (0.148), 0.3937 (0.175), 0.1214 (0.371)]
c $\hat{p}_{su}$ = [0.5830 (0.122), 0.2330 (0.255), 0.1840 (0.318)]
d $\hat{p}_f$ = [0.1103 (0.304), 0.5167 (0.105), 0.3730 (0.143)]

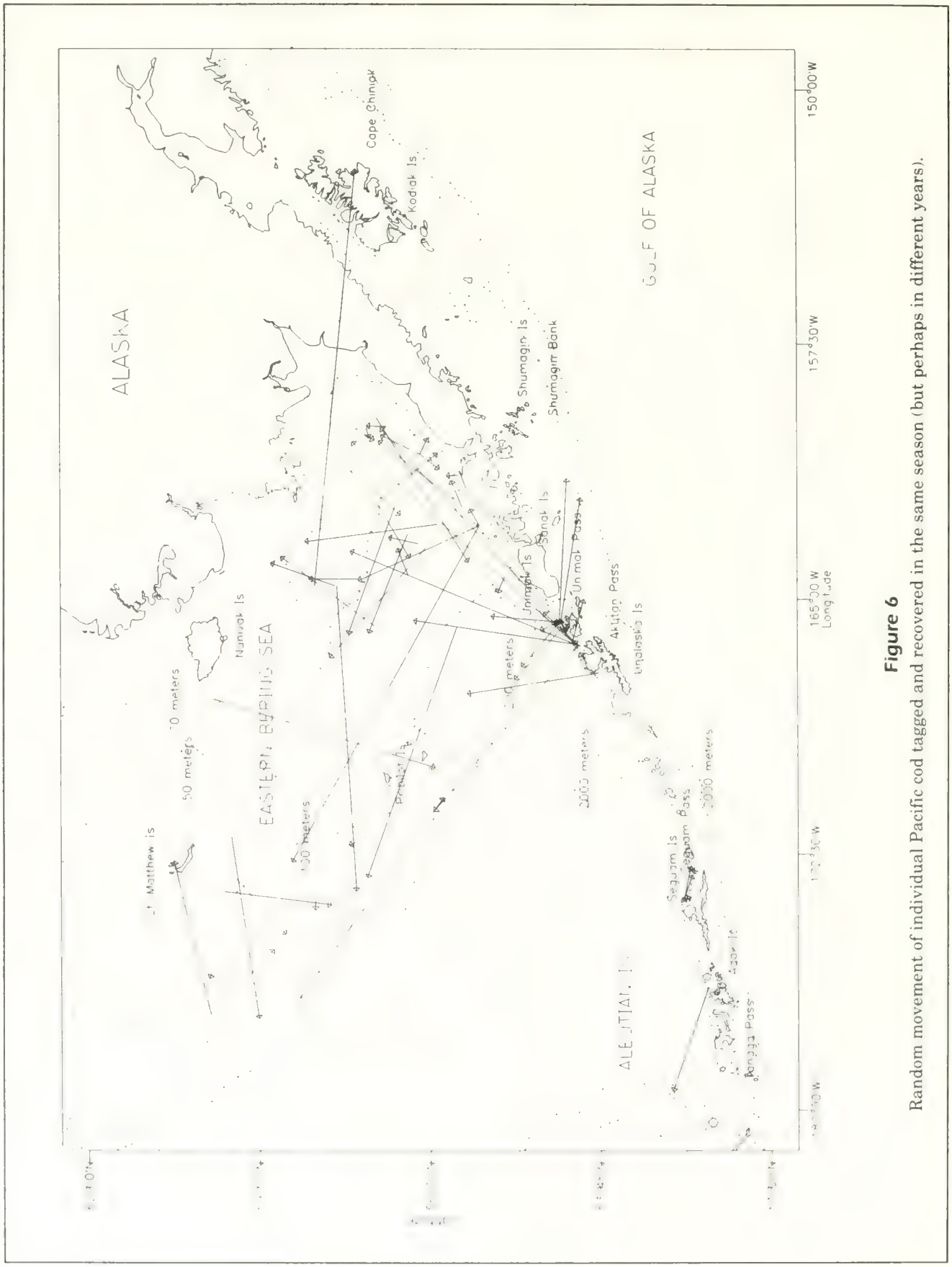

Figure 6

Random movement of individual Pacific cod tagged and recovered in the same season (but perhaps in different years).

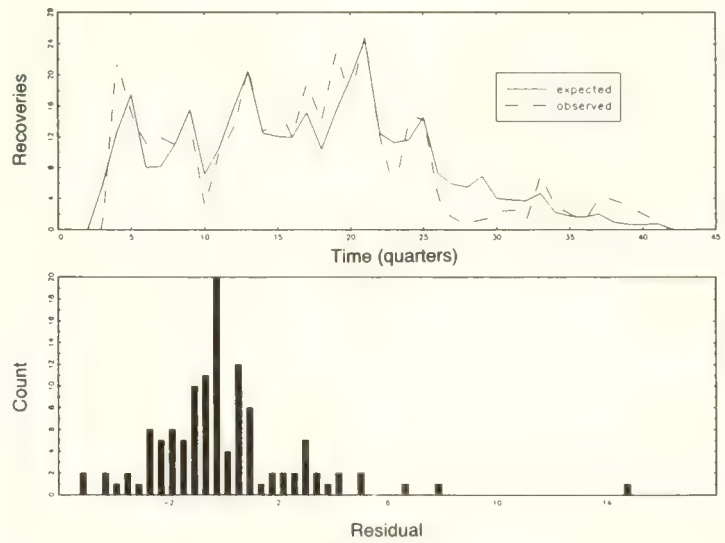

Figure 7

From the fit of the population dynamics model to the tagged Pacific cod population: graph of expected versus observed tag recoveries by quarter (**top**) and histogram of residuals by quarter and area (**bottom**).

(Hollowed and Low[4]) than the tagging data. Therefore, we conclude that observed movements in the tagged population generally reflect the population movements of Pacific cod in the eastern Bering Sea.

Emigration and immigration relative to the study area

We provide direct evidence that Pacific cod migrate from the eastern Bering Sea into the Gulf of Alaska. Of the 95 winter recoveries made in Area 3, 21 of these occurred in the Gulf of Alaska (Fig. 8; note that Fig. 8 includes 30 Gulf of Alaska recoveries from all seasons). Longline vessels operating in the winter quarter between Sanak Island and Shumagin Bank were the main source of returns. These data suggest that 22% of fish found in Area 3 in winter may migrate into the Gulf of Alaska. Multiplying this figure by the population dynamics estimate of 78% (which is the total eastern Bering Sea winter population within Area 3), or by the 68% of the winter commercial catch that is taken in Area 3, suggests that 15 to 17% of the total population in the eastern Bering Sea may migrate into the Gulf of Alaska during winter.

Table 4

Distribution of catch (numbers) by season and area (Area 1=the eastern Bering Sea shelf, Area 2=the outer eastern Bering Sea shelf and upper slope, Area 3= the main spawning area), from 1982 to 1992, for Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea. Estimated from the Alaska and Pacific Northwest Historical Groundfish Database (J. Berger, Alaska Fish. Sci. Cent., Seattle, WA 98115-0070, Personal commun., January 1993) and from the relative magnitude of trawl and longline catches.

Season	Area 1	Area 2	Area 3
Winter	0.085	0.235	0.680
Spring	0.496	0.393	0.111
Summer	0.703	0.276	0.021
Fall	0.176	0.651	0.173

A number of individual longer-range migrations tie together the Pacific cod population from 150° W to 180° W longitude (Fig. 8). We note with interest the recovery of two Bering Sea tags in the central Gulf of Alaska near Cape Chiniak on Kodiak Island, after 103 and 334 days. Other tagged Bering Sea emigrants have been recaptured on the North

[4] Hollowed, A. B., and L. L. Low. 1986. Productive gadoid fishing grounds based on species assemblage analysis. *In* M. A. Alton (ed.), A workshop on comparative biology, assessment, and management of gadoids from the North Pacific and Atlantic oceans. Proceedings: part II, p. 681-712. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., Bin C15700, Seattle, WA 98115-0070.

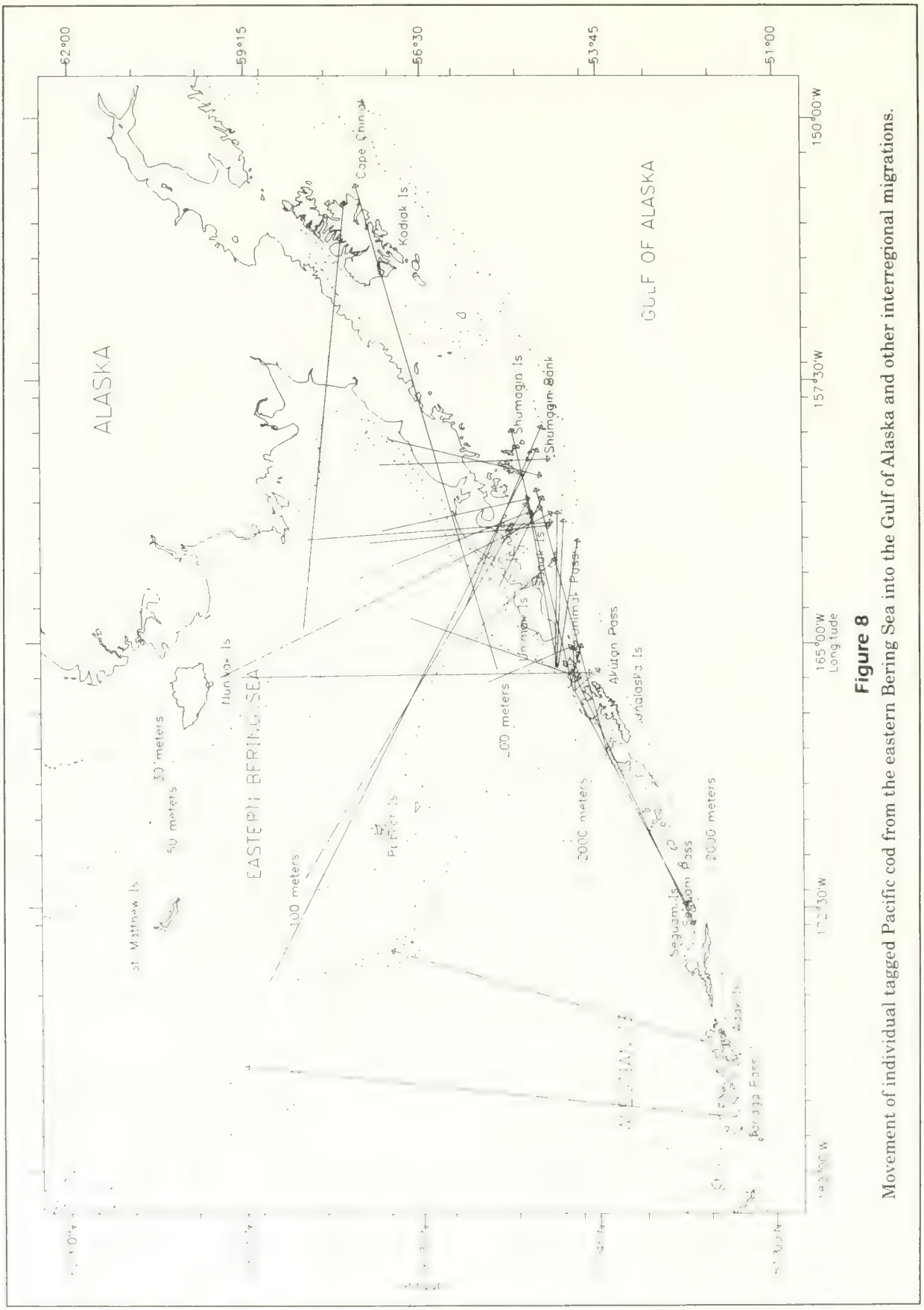

Figure 8

Movement of individual tagged Pacific cod from the eastern Bering Sea into the Gulf of Alaska and other interregional migrations.

Pacific side of Akutan Pass and Unimak Pass in the Aleutian Islands. Additionally, two fish tagged in the major spawning area (Area 3) were recaptured to the west in Seguam Pass within 250 days. In a striking occurrence of immigration to the Bering Sea, a pair of Pacific cod (65 cm fork length) tagged in Tanaga Pass near Adak Island were recaptured on the outer northwest shelf (above 57°N) after 3 and 5 years at liberty (Fig. 8).

Although substantial numbers of Pacific cod were tagged along the Aleutian Islands west of 170°W, including to about 174°E (Fig. 1), few recoveries have been made. These releases came from a single 1986 summer trawl survey and tagged fish were in poor condition because commercial foreign fishing operations were employed.

Discussion

Our analysis identified a seasonal circuit that we attribute to annual migrations for spawning and feeding; it also provided preliminary indications of emigration from the eastern Bering Sea. The former is described in terms of three eastern Bering Sea areas. The latter ties together more expansive distances as defined by regional geography or fishery management boundaries, or both (OCSEAP, 1987). Although the majority of tagged Pacific cod exhibited the seasonal character of short-term cross-shelf movements, a small number of tagged individuals provided empirical evidence for much longer transits.

We recognize that emigration and immigration probably occur with respect to the main study area (i.e. Areas 1–3). However, the locations of tag releases and numbers of tag recoveries received to date make it difficult either to quantify the amount of emigration from the eastern Bering Sea, or to conclude with certainty that return immigration to the eastern Bering Sea is significant. At this time, we believe there is some eastern Bering Sea immigration from the surrounding regions. However, considerable uncertainty exists because so few Pacific cod were tagged outside the study region, most importantly in the central and eastern Gulf of Alaska (Fig. 1). Also, we have some evidence that the western Aleutian Islands stock(s) may be fairly independent of the eastern Bering Sea, but this evidence is far from conclusive.

Despite these conjectures, statistics such as "distance traveled" and "rate traveled" versus "time at liberty" (Fig. 9) generally support our seasonal movement model. Observed "distance traveled" already is maximized within the first year of freedom. Similarly, observed "rate traveled" is maximized within the first year at liberty. This behavior is consistent

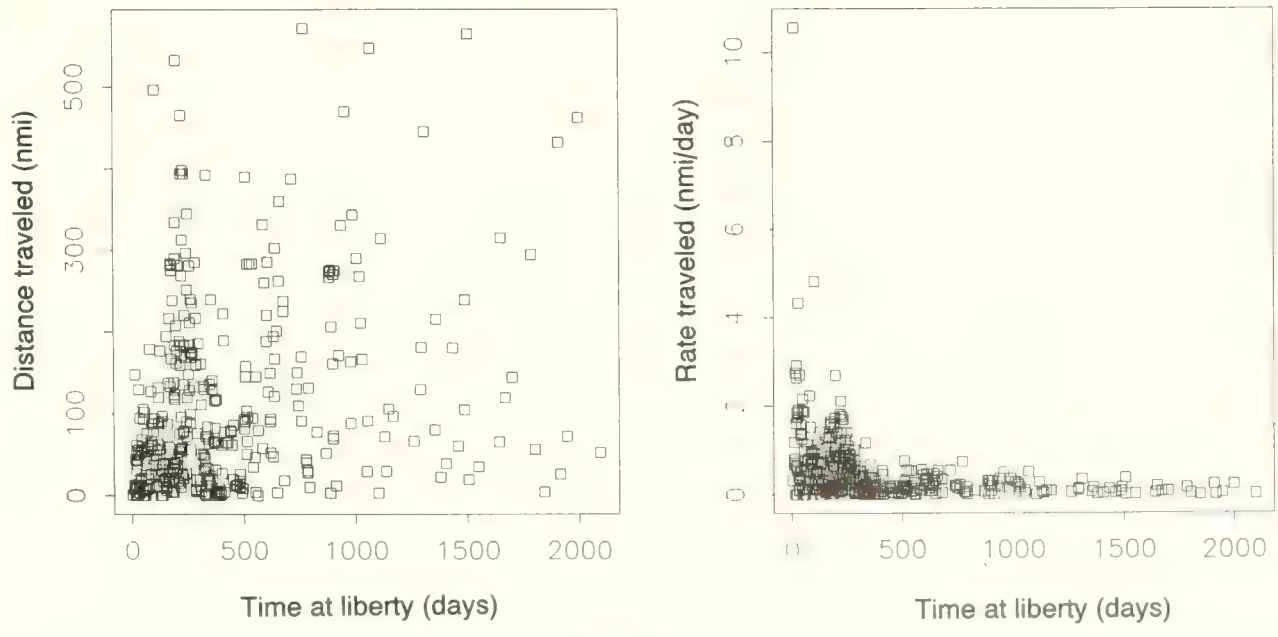

Figure 9

Scatter plots showing (**left**) the relationship between distance traveled (in nautical miles) and time at liberty and (**right**) the relationship between rate of travel and time at liberty for Pacific cod.

with seasonal migrations within a closed system. Other movements occur against a backdrop which is dominated by regular seasonal movements.

Movements of Pacific cod may be better understood in the context of the general life history, population dynamics and physical environment requirements of this species. Bakkala (1984) examined distribution patterns based on an analysis of research survey and commercial fishery catch per unit of effort and size composition data. He described a gradual shift over the southeast shelf with time, corresponding to a progression in cohort ages and the influence of year-class abundance. A tendency towards the offshore environment was noted from coastal waters to the outer shelf and slope edge. This was based on an areal transition stemming from ontogenetic development in younger age (1–3 yr) to older age (4+ yr) groups. Further, during years of higher than average abundance, the population range was much more extensive than that in years of low abundance (Bakkala, 1984).

From Russian trawl surveys, Stepanenko[5] described winter concentrations along the upper slope at depths between 400 and 545 m. Prespawning and spawning aggregations were consistently found northwest of Unimak Island, in the Pribilof Islands sector, and along the northern slope on either side of the U.S.-Russia Convention Line. The most significant spawning aggregations occurred in the vicinity of Unimak Pass along the outer shelf edge.

The literature indicates that preferred water temperatures (0 to 10°C) are the primary factor for determining centers of Pacific cod abundance. Towards its southern range off British Columbia, Ketchen (1961) reported highest catch rates at bottom temperatures of between 6 and 9°C. Off Russia, Moiseev (1953) noted that spawning Asian Pacific cod preferred 80–290 m depths and water temperatures between 0 and 2 to 3°C; optimal summer temperatures were between 0.2 and 4.5°C. Hirschberger and Smith (1983) reported water temperatures around 5.4°C for spawning Gulf of Alaska Pacific cod at 150–250 m.

In the eastern Bering Sea, high winter concentrations of Pacific cod coincide with warmer water (mean 4.0°C) found year-round in depths off Unimak Pass and the upper slope (Kihara, 1982, a and b; Bakkala, 1984). Bottom temperatures on the shelf drop from the 0.2 to 4.5°C range in summer to below 0°C in winter (Schumacher and Reed, 1983). Thus at the high latitudes of the Bering Sea, the stimulus for offshore migration appears to be avoidance of the intense cooling of inshore waters that accompany advancing ice formation from the Bering Strait in favor of warmer temperatures at depth. The spring feeding migration, shoreward, is most likely timed to the warming of the coastal shelf environment and a return to summer norms (Bakkala, 1984).

Interestingly, at lower latitudes, seasonal migrations are reversed. At the southernmost edge of its range, off Korea, Japan, and in Puget Sound, Washington (Karp, 1982; Mishima, 1984; Zhang, 1984), Pacific cod migrate to deep offshore waters during summer months to avoid excessively heated (>10°C coastal waters. A returning inshore spawning migration occurs each winter.

Moiseev (1953) noted very limited along-shore migrations in Russian waters. However, active seasonal migrations between coastal shallows and offshore depths perpendicular to the shoreline (mainly in response to inshore and offshore temperature shifts) were found. He further hypothesized that the potential for stock intermingling was reduced because of limited along-shore movement. Winter offshore movements were observed throughout the northern range of Pacific cod. Local abundance centers were always in the direction of the preferred temperature regime in response to the pronounced cooling of their onshelf environment. Westrheim (1984) noted that Pacific cod off Vancouver Island, British Columbia, exhibited the same bathymetric seasonal movements as Pacific cod in Alaska but very limited along-shore movements.

In all of the cases described above, seasonal migrations of Pacific cod appear to be triggered by the desire to avoid temperature extremes that accompany the changing seasons. In the eastern Bering Sea, movements represent necessarily long-range migrations across the Bering Sea shelf which on average is 300 nmi wide. For southern coastal stocks, the same result can be achieved with much shorter offshore migrations to depth. It is likely that interregional along-shore migrations seldom are found because they are unnecessary for achieving the preferred temperature regime (Moiseev, 1952).

Rose (1993) found a similar pattern in Atlantic cod, *Gadus morhua,* based on hydroacoustic surveys. He attributed seasonal movement to springtime feeding migrations, which shifted Atlantic cod from offshore winter spawning grounds shoreward. Migration pathways were facilitated by stable bottom temperature regimes (2–3°C) associated with trenches on the northeastern Newfoundland shelf.

How large-scale stock structure is affected by migrations motivated by preferred temperatures is unclear. Grant et al. (1987) screened Pacific cod genetic samples from throughout their range. Two ge-

[5] Stepanenko, M. A. 1989. Condition of stocks, interannual variability of catch per unit of effort and fishing of cod in the eastern part of the Bering Sea. Pacific Research Institute of Fisheries and Oceanography (TINRO), Vladivostok, USSR. Document submitted to the US-USSR bilateral meetings, November 1989, 35 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., Bin C15700, Seattle, WA 98115-0070.

netically distinct stocks were detected: a western North Pacific Ocean (Asian) group, and an eastern North Pacific group which included the Bering Sea, Aleutians Islands, and Gulf of Alaska regions. There were virtually no regional genetic differences among any of the North American samples. These authors were unable to identify where the effective northern boundary between the western and eastern groups lies, though the western Bering Sea was considered most likely. Grant et al. (1987) attributed this lack of genetic differentiation to gene flow between various subareas and regions on either side of the Pacific. Grant et al. (1987) were puzzled that most of the literature on Pacific cod pointed toward locally isolated stocks (Moiseev, 1953; Svetovidov, 1948; Ketchen, 1961; Wilimovsky et al., 1967). Our tagging study confirms sufficient migration to explain Grant et al.'s findings of genetic homogeneity in Pacific cod over broad areas of the North Pacific.

We have confirmed from tagging that Pacific cod migration occurs between the Bering Sea and Aleutian Islands. Because of the experimental design, the majority of tag returns demonstrate emigration from the Bering Sea but have not shown conclusively that immigration to the Bering Sea takes place. Even so, this study shows that significant exchange may occur within the open ocean populations of Pacific cod off Alaska. Whether Bering Sea Pacific cod have a reciprocal exchange to the wider Gulf of Alaska beyond the nearby waters of major Aleutian passes remains an open question. Lack of data precludes any further statement or quantification of exchanges between these regions. Further elucidation must await additional tagging results, particularly from the eastern Gulf of Alaska and western Aleutian Islands.

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Literature cited

Bakkala, R. G.
1984. Pacific cod of the eastern Bering Sea. Int. N. Pac. Fish. Comm. Bull. 42:157–179.

1993. Structure and historical changes in the groundfish complex of the eastern Bering Sea. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 114, 91 p.

Bakkala, R. G., S. Mishima, S. J. Westrheim, C. I. Zhang, and E. S. Brown.
1984. Distribution of Pacific cod in the North Pacific Ocean. Int. N. Pac. Fish. Comm. Bull. 42:111–115.

Fienberg, S. E.
1977. The analysis of cross-classified categorical data. The MIT Press, Cambridge, MA, 151 p.

Grant, W. S., C. I. Zhang, T. Kobayashi, and G. Stahl.
1987. Lack of genetic stock discretion in Pacific cod (*Gadus macrocephalus*). Can. J. Fish. Aquat. Sci. 44:490–498.

Heifetz, J., and J. Fujioka.
1991. Movement dynamics of tagged sablefish in the northeastern Pacific. Fish. Res. 11:355–374.

Hilborn, R.
1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can. J. Fish. Aquat. Sci. 47:635–643.

Hirschberger, W. A., and G. B. Smith.
1983. Spawning of twelve groundfish species in the Alaska and Pacific coast regions, 1975–1981. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-44, 50 p.

Karp, W. A.
1982. Biology and management of Pacific cod (*Gadus macrocephalus*) in Port Townsend, Washington. Ph.D. diss., Univ. Washington, Seattle, WA, 119 p.

Ketchen, K. S.
1961. Observations on the ecology of the Pacific cod (*Gadus macrocephalus*) in Canadian Waters. J. Fish. Res. Board Can. 18:513–558.

Kihara, K.
1982a. Fluctuations of the water temperature and the salinity in the eastern Bering Sea. Bull. Jpn. Soc. Sci. Fish. 48(12):1685–1688.

1982b. Influences of the marine environment upon the formations of the benthic species community in the eastern Bering Sea. Bull. Jpn. Soc. Sci. Fish. 49(1):49–54.

Kimura, D. K., and J. J. Lyons.
1990. Choosing a structure for the production ageing of Pacific cod (*Gadus macrocephalus*). Int. N. Pac. Fish. Comm. Bull. 50:9–23.

Kimura, D. K., A. M. Shimada, and S. A. Lowe.
1993. Estimating sablefish (*Anoplopoma fimbria*) and Pacific cod (*Gadus macrocephalus*) von Bertalanffy growth parameters using tag-recapture data. Fish. Bull. 91:271–280.

Low, L. L. (ed.).
1991. Status of living marine resources off Alaska as assessed in 1991. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-221, 95 p.

Mishima, S.
1984. Stock assessment and biological aspects of Pacific cod (*Gadus macrocephalus* Tilesius) in Japa-

nese waters. Int. N. Pac. Fish. Comm. Bull. 42:116–129.

Moiseev, P. A.
1952. Some characteristics of the distribution of bottom and demersal fishes of far eastern seas. Izv. Tikhookean. Nauch-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 37. [Transl. Fish. Res. Board Can., Transl. Ser. 94.]
1953. Cod and flounder of the far eastern seas. Izv. Tikhookean. Nauch-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 40. [Transl. Fish. Res. Board Can., Transl. Ser. 119.]

NMFS (National Marine Fisheries Service).
1992. Our living oceans: report on the status of U.S. living marine resources, 1992. NOAA Tech. Memo. NMFS-F/SPO-2, 148 p.

OCSEAP (Outer Continental Shelf Environmental Assessment Program).
1987. Marine Fisheries: resources and environments. *In* D. W. Hood and S. T. Zimmerman (eds.), The Gulf of Alaska—physical environment and biological resources, p. 417-458. U.S. Government Printing Office, Washington, D.C. 20402.

Rose, G.A.
1993. Cod spawning on a migration highway in the north-west Atlantic. Nature 366:458–461.

Schumacher, J. D., and R. K. Reed.
1983. Interannual variability in the abiotic environment of the Bering Sea and Gulf of Alaska. *In* W.S. Wooster (ed.), From year to year, p. 111–133. Univ. Washington, Coll. Ocean Fish. Sci., Wash. Sea Grant Program, Sea Grant publ. WSG-WO 83-8.

Shimada, A. M.
1985. A study of eastern Bering Sea Pacific cod: resource assessment, fishery development and management under variable recruitment. M.M.A. thesis, Univ. Washington, Seattle, WA, 212 p.

Svetovidov, A. N.
1948. Gadiformes. Acad. Nauk. SSSR, Zool. Inst., Fauna SSSR, Ryby 9(4), N.S. 34, 304 p. [Transl. Israel Program Sci. Transl., 1962. Available from U.S. Dep. Commer. Natl. Tech. Inf. Serv., Springfield, VA, as OTS 63-11071.]

Teshima, K.
1985. Maturation of Pacific cod in the eastern Bering Sea. Bull. Jpn. Soc. Sci. Fish. 51(1):29–31.

Thompson, G. G.
1994. Pacific cod. *In* L. L. Low (ed.), Status of living marine resources off Alaska, 1993, p. 14–16. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-27, 110 p.

Westrheim, S. J.
1984. Migrations of Pacific cod (*Gadus macrocephalus*) in British Columbia and nearby waters. Bull. Int. N. Pac. Fish. Comm. 42:214–222.

Wilimovsky, N. J., A. Peden, and J. Peppar.
1967. Systematics of six demersal fishes of the North Pacific Ocean. Fish. Res. Board Can. Tech. Rep. 34:1–95.

Zhang, C. I.
1984. Pacific cod of South Korean waters. Bull. Int. N. Pac. Fish. Comm. 42:116–129.

Abstract.—The chemistry of calcified tissues has been suggested as a source of useful information on the population structure and environmental histories of fishes. We evaluated this possibility by examining in detail regional and ontogenetic variability in the chemical composition of sagittae of juveniles and adults of the temperate marine groundfish *Nemadactylus macropterus*. Six elements (in order of decreasing abundance, Ca, Na, Sr, K, S, and Cl) were consistently detected in the sagittae at concentrations greater than 200 ppm; all exhibited levels of individual, ontogenetic, and regional variability well in excess of their respective scales of measurement error. Comparisons of juveniles and adults from different sites indicate that composition of the otolith is most alike in fish from adjacent sites, that most juveniles are similar to adults collected from the same site, and that the differences in composition that characterize sites are manifest during most, if not all, of the fish's ontogeny. These results are consistent with the hypotheses that otolith composition reflects population structure and that these populations are largely self-recruiting. However, the results also suggest that the chemical composition of otoliths is much less sensitive to environmental conditions than previously thought. Rather, it appears that regional differences in composition either have a genetic basis or are set by environmental influences early in life and are then maintained throughout subsequent life history.

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An evaluation of electron-probe microanalysis of otoliths for stock delineation and identification of nursery areas in a southern temperate groundfish, *Nemadactylus macropterus* (Cheilodactylidae)

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Knowledge of geographic structure is fundamental to understanding the dynamics of marine fish populations (e.g. Sinclair, 1987). Nonetheless, even for the small number of species thus far investigated, there remains considerable uncertainty regarding population structure. This is due to the lack of a widely applicable, direct means of mapping how far and in what directions larvae disperse. A variety of indirect techniques have been applied to the problem, e.g. modelling larval advection from oceanographic features, analyzing parasite loads, mapping phenotypic characters, and locating and enumerating discrete spawning areas. However, all are limited in scope and in the strength of the inferences that can be drawn from them. For this reason, the geographic structure of marine populations is usually inferred from genetic studies (e.g. Avise et al., 1987; Waples and Rosenblatt, 1987; Smith et al., 1990). But genetic techniques are also far from ideal for this task: they will not detect differences in the face of even low levels of larval or adult mixing among populations (Hartl and Clark, 1989); they cannot directly measure rates of individual exchange among sites or, usually, specify the origin of individuals; and results from even a successful study can be ambiguous, i.e. a genetic difference between sites suggests little dispersal, but the lack of any difference is largely uninformative. Such difficulties have prompted continuing research into alternative, and perhaps more definitive, techniques for evaluating population structure.

One alternative technique is the analysis of the chemical composition of calcified structures. As early

as 1967 (Fisheries Agency of Japan, 1967), preliminary studies suggested that the quantitative analysis of the microconstituents and trace elements in otoliths, vertebrae, and scales could provide information on population structure and the movements of individual fish. This suggestion was based on two assumptions and a hypothesis. The assumptions were that 1) the calcified structures are not susceptible to dissolution or resorption and 2) the growth of these tissues continues throughout life. If these assumptions are correct, calcified structures are permanent records of the influence of endogenous and exogenous factors on their calcium-protein matrices. The hypothesis is that differences in the environments to which fish in each population are exposed affect the incorporation of elements in calcified structures, which results in chemical compositions specific to each population. An extensive fisheries literature supports the assumptions for otoliths, if not perhaps for scales and vertebrae (e.g. Sauer and Watabe, 1989). The working hypothesis also appears reasonable, given an extensive literature on invertebrates that relates differences in the composition of, for example, mollusc shells, and coral skeletons to a range of environmental and physiological conditions (Thompson and Livingston, 1970; Weber, 1973; Houck et al., 1977; Buchardt and Fritz, 1978; Smith et al., 1979; Rosenberg, 1980; Schneider and Smith, 1982).

Since 1967, several studies have investigated whether the composition of calcified structures indicates stock or subpopulation identity in fishes (e.g. Klokov and Frolenko, 1970; Calaprice, 1971, 1985; Calaprice et al., 1971, 1975; Bagenal et al., 1973; Gauldie and Nathan, 1977; Behrens Yamada et al., 1987; Lapi and Mulligan, 1981; Mulligan et al., 1983, 1987; Edmonds et al., 1989; Calaprice[1]), using a variety of analytical techniques (see reviews by Coutant, 1990; Gunn et al., 1992). The results have been mixed. In part, this is because most techniques used required a relatively large amount of material for analysis. Otoliths or bones from many individuals often had to be pooled to reach the minimum sample mass required. Because individual and ontogenetic variability could not be addressed, it has been difficult to assess the potential of the approach.

In 1987, we began experiments with a view to using fine-scale, ontogenetic variation in the composition of fish otoliths as an indicator of movement and migration patterns. The results of the first step — an investigation of the operating characteristics of probe microanalyzers as they affect data quality and the development of reliable techniques for 'life history scans' across otoliths — are reported in Gunn et al. (1992) and Sie and Thresher (1992). In this paper, we evaluate the extent to which otolith composition in a test species varies ontogenetically, among individuals within sites, and among sites, in order to assess whether such variation is of sufficient magnitude for, and contributes to, resolving population structure in the species.

The species chosen for study was the jackass morwong, *Nemadactylus macropterus* (Cheilodactylidae), a moderate-sized (maximum about 70 cm standard length), bottom-dwelling fish common on the middle and outer continental shelf off southern Australia, New Zealand, South Africa, and the Pacific coast of South America (Robertson, 1978). The species was chosen for two reasons. First, the population structure of the species in Australian waters is contentious. On the one hand, regional declines in catch rates suggest localized stocks, which is consistent with work in New Zealand, where the species has three geographically discrete populations (Gauldie and Nathan, 1977; Robertson, 1978) . On the other hand, a small amount of tagging data for adults (Smith, 1989), allozyme data for specimens collected in southeast Australia (Richardson, 1982), and recent allozyme and mitochondrial DNA analyses for the entire Australian range (Elliott and Ward, 1994; Grewe et al., in press) suggest a single, broadly distributed population (Smith, 1989; Tilzey et al., 1990). This interpretation also appears to be consistent with the early life history of the species: *N. macropterus* spawns along the middle continental shelf, has a planktonic duration of 9–12 months, and has a morphologically specialized late-stage larva ('paper fish') that is neustonic and generally caught offshore of the continental shelf (Vooren, 1972). This combination is taken to imply high rates of local mixing during the larval stage.

Nemadactylus macropterus was also chosen because of uncertainty about the location of its nursery areas in Australia. To date, the only place in Australia where large numbers of juveniles have been found is the shallow bays and inlets of southeastern Tasmania. As a result, it has been suggested that this area is a critical habitat supporting the entire Australian population (Tilzey et al., 1990). Given continuing coastal development in this area, if the hypothesis is correct, conservation measures need to be developed and implemented to ensure the continued viability of the fishery.

Analysis of otolith composition could help resolve both questions. With regard to population structure, we hypothesized that if there are discrete spawning populations in Australian waters, then the composition of the central, first-forming portion of the otolith

[1] Calaprice, J. R. 1983. X-ray fluorescence study of stock variation in bluefin tuna. Status report submitted to NMFS, Miami, March 1983, 60 p.

would differ geographically. With regard to the number and location of nursery areas, we further hypothesized that if there is only one nursery area, then the composition of that part of the otolith deposited during residence in the nursery ground would be similar for all adults, irrespective of where they were caught, and would match that of juveniles caught in southeastern Tasmania.

Methods

Collection details for juvenile and adult *N. macropterus* are provided in Figure 1 and Table 1. Recently settled (0+) juveniles were collected by hand-lining and trawling at six sites off Tasmania and southern Victoria. Adult specimens were also obtained at six sites, from commercial and scientific trawls on the southeastern Australian continental shelf. To minimize possible effects of interannual variation in otolith composition, we minimized the number of year classes in the sample by using only adults in the size range of 30–35 cm fork length. Otolith macrostructure and published length-at-age keys for the species (Smith, 1982) suggest that the specimens were a mixture of the 1980 to 1984 year classes and that year-class distributions overlapped broadly among sites. The juveniles were from the 1987 and 1988 year classes.

All specimens were frozen at –20°C shortly after collection and remained frozen (up to 30 days) until the otoliths were removed. After extraction, each otolith was cleaned of adhering tissue with fine forceps and a soft-bristled brush in millepore-filtered distilled water. They were then dried in an oven at 40–45°C for at least 6 hours, after which they were stored in polyurethane capsules in a desiccating cabinet.

Procedures for embedding, sectioning, and preparing otoliths for probe microanalysis are detailed in Gunn et al. (1992). Only sagittae were used in this study, because of their larger size. Prior to embedding, a scaled diagram of the distal surface of each otolith was made in order to guide subsequent sectioning. The otolith was then fixed upright on its ventral edge to the base of an embedding mold with a drop of Araldite. The mold was then filled with a harder-setting resin. After hardening, the otolith was sectioned with a diamond-edged saw blade (350 µm thick) on a rotary saw. Grinding to the plane of the primordium was done by hand with 2400-grade silicon carbide wet/dry paper. Final polishing was done by using progressively finer grades of diamond paste (6–3 µm) and aluminum oxide powder (Linde B) on a lapping machine. After polishing, the section was ultrasonically cleaned and stored in a moisture-free environment. Prior to probe microanalysis, the section was heated on a hot-plate at 80°C for 10 min-

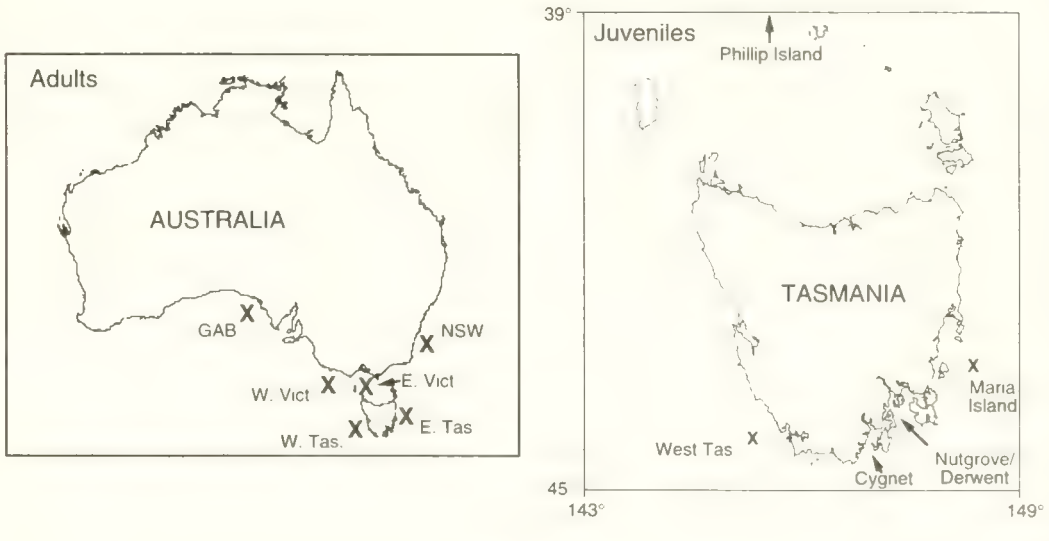


Figure 1

Source locations of samples of adult and juvenile *Nemadactylus macropterus* examined by electron probe microanalysis. Sample details are provided in Table 1. Adult sites: GAB=Great Australian Bight, W. Vict.=western Victoria; E. Vict.=eastern Victoria; W. Tas.=western Tasmania; E. Tas.=eastern Tasmania; and NSW=New South Wales. Nutgrove and Derwent are two inshore sites sampled for juveniles, both located in the Storm Bay (SE Tasmanian) estuary. Phillip Island is an inshore site off Victoria.

utes to remove any residual moisture, coated with a 250–300 Å (measured by color on brass) coat of carbon with a sputter coater, and then stored under vacuum until insertion into the probe.

The procedures used to analyze otolith composition are detailed in Gunn et al. (1992). Damage to the specimens under the electron beam is inevitable. The amount of damage, and hence quality of the data, is proportional to beam-power density (i.e. beam current × accelerating voltage/ target area). In Gunn et al. (1992), we concluded that beam power densities greater than 3.0 $\mu W \cdot \mu m^{-2}$ resulted in unacceptable levels of specimen damage, data precision, and accuracy. Hence, data for the current study were acquired by using the following beam conditions: 25 nA current, 15 kV accelerating voltage, a 14 μm diameter 'defocused' beam (and hence a beam power density of 2.44 $\mu W \cdot \mu m^{-2)}$ and a total acquisition time of 3 minutes, 42 seconds per point. Comparisons of parallel scan lines (see Fig. 6) included some analyses at a 6 μm beam diameter, 5.5 nA current, and 15 kV accelerating voltage; despite the small beam diameter, beam power density for this series (2.92 $\mu W \cdot \mu m^{-2}$) is within our 'safe' limit. The electron probe microanalyzer used was a Cameca Camebax fitted with three wave-length dispersive detectors. The concentrations (weight-fractions) of Na (sodium), K (potassium), Ca (calcium), S (sulphur), and Cl (chlorine) were calculated based on the count rates measured for their respective K_α lines, and for Sr (stron-

Table 1

Collection details for *Nemadactylus macropterus* adults and juveniles analyzed in this study.

Location	Date collected	Collection method	Sample size	Size range (cm FL)
Adults				
NSW (Lat.34°40'S Long.151°10'E)	12 Jan 90	Trawl	11	36.0–38.0
W. Victoria (Lat.38°34'S Long.141°10'E)	30 Aug 87 –6 Sep 87	Trawl	6	34.6–37.1
E. Victoria (Lat.37°48'S Long.139°45'E)	6 Dec 89	Trawl	17	27.7–35.5
E. Tasmania (Lat.42°40'S Long.148°15'E)	16 April 89 15 Nov 89	Trawl Trawl	2 11	30.7–33.0 32.0–38.0
W. Tasmania (Lat.43°07'S Long.145°32'E)	21 Mar 89	Trawl	5	30.3–35.4
GAB (Lat.33°25'S Long.125°56'E)	15 Oct 89	Trawl	16	28.0–35.0
Juveniles				
Cygnet (Lat.43°10'S Long.147°05'E)	19 Dec 87 3 Dec 88	Hand-line Hand-line	27 13	8.6–11.6 8.3–13.6
Derwent (Lat.42°53'S Long.147°20'E)	25 Sep 87 9 Nov 87	Hand-line Hand-line	9 11	13.4–17.8 15.8–16.7
W Tasmania (Lat.43°07'S Long.145°32'E)	21 Mar 89	Trawl	26	9.8–18.1
Maria Island (Lat.42°31'S Long.148°10'E)	7 April 88	Trawl	11	12.0–15.8
Nutgrove (Lat.42°55'S Long.147°21'E)	29 Mar 88	Trawl	9	14.6–16.1
Phillip Island (Lat.38°35'S Long.145°10'E)	13 Dec 87	Trawl	10	9.0–18.0

tium), the L_α line. S and Cl were measured on Spectrometer 1 (PET), K and Ca on Spectrometer 2 (PET), and Na and Sr on Spectrometer 3 (TAP). Matrix corrections were made by using the "PAP" (Pichou and Pichoir, 1984) matrix conversion software. Minimum detection limits and confidence intervals for the concentration estimates are based on equations provided by Ancey et al. (1978).

Ontogenetic variation in composition was assessed by analyzing a series of points along the longest growth axis of each otolith section—a "life history scan." The finished section of the sagitta of *N. macropterus* exposes a nearly straight, uninterrupted growth axis, through which we ran a series of programmed scan lines that tracked the slight curvature of the axis (Fig. 2). We duplicated this axis as closely as possible in each specimen in order to maximize comparability of the data sets. The life history scan line for each fish ran from the primordium to the posterior ventral tip of the otolith. The size of the scan points and their spacing were determined by logistic considerations and, in part, by the results of experimental trials. In practice, routine spacing (center to center) between points was 25 μm. In the case of the parallel scans (see Fig. 6), we used a beam diameter of 14 μm spaced 16 μm apart and 6 μm diameter beams spaced 8 μm apart. Reproducibility of life history scan data was evaluated by comparing left and right otolith pairs from the same fish.

Even if the data are free from conspicuous distortions due to irregular surface features, the use of data from a single-point probe analysis for evaluation of stock structure still risks high error rates due to measurement noise (Gunn et al., 1992). Consequently, we analyzed stock structure in two ways: based on comparisons of single-point data collected adjacent to the primordium (point 2); and based on mean concentrations of the first five probe points adjacent to the primordium (points 2–6 inclusive). The latter method filters out high-frequency measurement noise but risks low discriminant power by including information from relatively late in larval life. Point 6 is about 125 μm from the primordium; increment counts suggest this corresponds to a larval age of about 45–55 days.

Statistical procedures in general follow Sokal and Rohlf (1981). Test for normality were made by using Lilliefors *K-S* test. Differences in mean concentrations among sites were tested by means of a Kruskal-Wallis nonparametric ANOVA. Groupings of sites and specimens were tested and quantified by linear discriminant function analysis (LDFA) with the SYSTAT statistical software package. General procedures for and assumptions underlying LDFA are described by Klecka (1980); Cameron (in press) reviews the application of discriminant analysis to studies of otolith and skeletal composition.

Results

Composition of *N. macropterus* otoliths; data quality and reproducibility

Six elements could be reliably detected in *N. macropterus* otoliths by wavelength-dispersive electron probe microanalysis (WD-EPMA): Ca, Na, Sr, K, S, and Cl, in order of decreasing mean concentration. The elements in *N. macropterus* sagittae constitute three distinct sets separated in concentration from other less abundant elements by a difference of one to three orders of magnitude (Fig. 3): Ca, carbon, and oxygen (the last two are not routinely measured because of methodological difficulties) constitute the 'macro-constituents' present in concentrations >10% (10^5 ppm) by weight; Na, Sr, K, S, and Cl constitute the 'micro-constituents,' which occur in mean con-

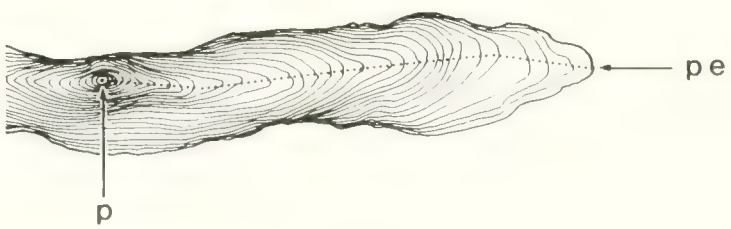


Figure 2

Diagram of section of a sagitta of an adult *Nemadactylus macropterus*, as prepared for electron probe microanalysis, depicting programmed transects used to analyze points along the main growth axis from the primordium (p) to the otolith's posterior edge (pe).

Table 2

Minimum detection limits (MDL), mean and ranges of estimated concentrations, and measurement error for *Nemadactylus macropterus*, of the six elements that could be assayed reliably with a WD electron probe. The values are based on a random subset of our data (n = 478 points), including numerous individuals and positions along the scanned axis of points analyzed. Concentrations are given in ppm (by weight), except for Ca which is in percent of the target mass. Note that values below the minimum detection limit are effectively zero. 'Minimum significant difference' is based on comparison of 'replicate' points in parallel life history scans (see text). CI = Confidence interval.

Element	MDL	Mean (range) concentrations	Measurement error (absolute, %)	Minimum significant difference	
				Mean (range)	99% CI
Ca	—	38.8% (35.3–44.5)	—	—	—
Sr	311	2240 (1430–3860)	±157 (7%)	210 (12–964)	331
Na	159	3331 (2680–4240)	±122 (3.7%)	160 (10–450)	235
K	136	729 (280–1630)	± 72 (10%)	77 (0–320)	118
S	149	421 (220–1220)	± 76 (18%)	80 (4–247)	121
Cl	157	255 (0–1230)	± 72 (28%)	48 (10–210)	73

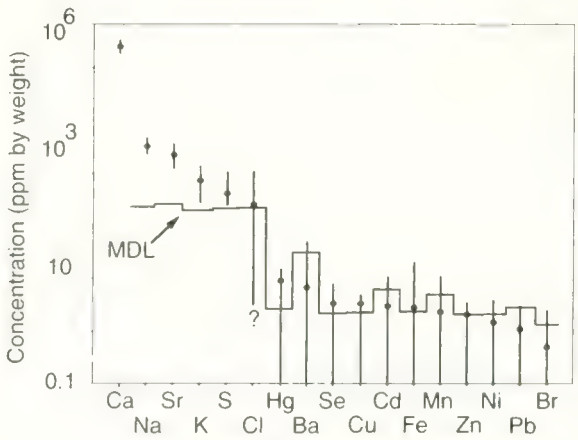


Figure 3

Mean (solid circle) and ranges (vertical line) of concentrations of the elements detected in the sagittae of *Nemadactylus macropterus* by means of electron probe (for Ca, Na, Sr, K, S, and Cl) and proton probe (for mercury (Hg), barium (Ba), selenium (Se), copper (Cu), cadmium (Cd), iron (Fe), manganese (Mn), zinc (Zn), nickel (Ni), lead (Pb), and bromine (Br)) microanalyses. For proton probe methodology and results, see Sie and Thresher (1992). Data are a compilation of >500 points across numerous individuals and positions along the growth axis. The minimum detection limit (MDL) for each element is indicated by the irregular horizontal line and is based on the standard output of the respective probe microanalyzers at our standard operating conditions (see Gunn et al., 1992; Sie and Thresher, 1992). The minimum concentration of Cl is below the detection limit of the electron-probe microanalyzer but could not be determined with the more sensitive proton-probe microanalyzer because of our operating conditions (see Sie and Thresher, 1992).

centrations of 100–5000 ppm; and a variety of 'trace elements' (e.g. iron, copper, and bromine) occur at concentrations <10 ppm. Only the micro-constituents and Ca can be measured accurately by WD-EPMA. Absolute ranges of concentrations, measurement error (absolute and 95% confidence intervals), and minimum detection limits (MDL's) for each of these elements are given in Table 2. Measurement error is inversely correlated with mean concentration, ranging from 3.7% in Na to 28% in Cl. Of the six elements measured, only Cl occurred occasionally at less than its respective MDL (157 ppm). Although the microanalyzer reports values less than the MDL, these values were considered noise and set equal to zero for analyses of population structure.

Life history scans for three fish chosen randomly from the data set (Fig. 4) illustrate several points typical of our data. First, all six elements vary ontogenetically in concentration well in excess of the uncertainty associated with measurement. Second, concentrations at any given position correlate strongly with those at neighboring points; for all six elements, autocorrelations are highly significant at scales <100 µm (e.g. Fig. 5), which suggests that in *N. macropterus* this is the typical scale of ontogenetic variability in composition. Comparison of 'small spot-closely spaced' analyses (6 µm beam diameter spaced at 8 µm intervals) with 'large spot-widely spaced' analyses (14 µm diameter at 16 µm spacing) suggests that a sampling scale finer than our standard analysis reveals few, if any, major variations in otolith composition that would not be detected at the coarser sampling scale (Fig. 6). Third, absolute variability is highest for Sr, which can vary within specimens over half an order of magnitude. However, relative variability is as high in S and Cl; coefficients of

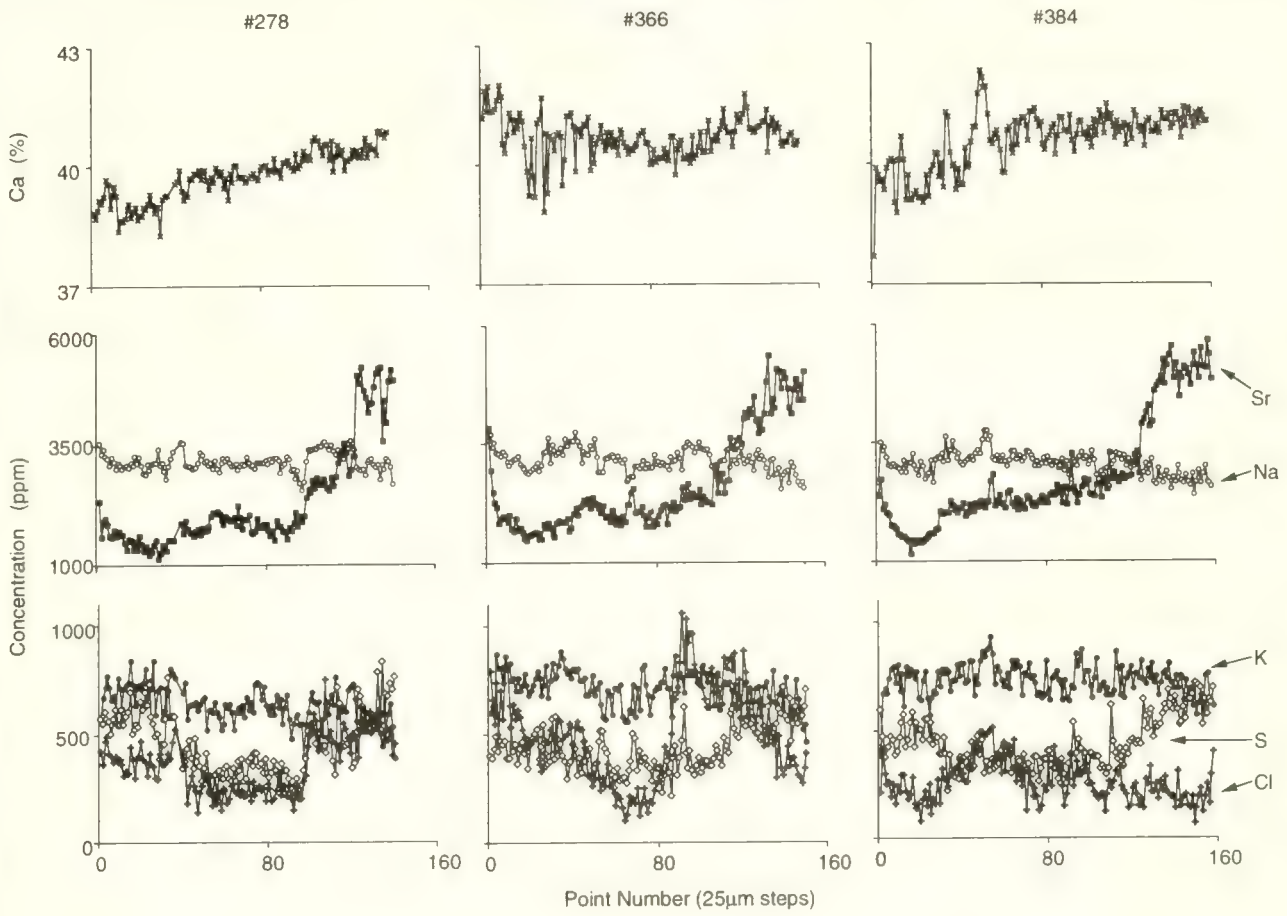


Figure 4

Cross-otolith (primordium to posterior margin) variation in the measured concentrations of the six elements (Ca, Na, Sr, K, S, and Cl) that could be reliably measured by WD electron-probe microanalysis in *Nemadactylus macropterus* sagittae. Concentrations are reported in units of ppm by weight for all elements other than Ca, which is reported as percent by weight. Data are adjusted to standards and cleaned of effects of surface pitting and cracks but are otherwise unfiltered. Specimens were chosen randomly from the adult data set and appear to be representative of the variation observed.

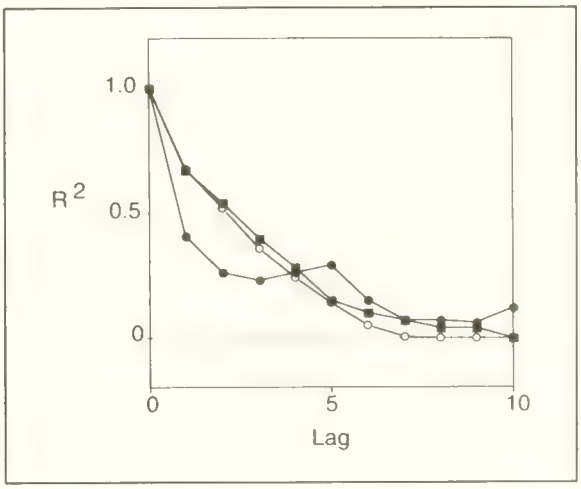


Figure 5

Auto-correlation analysis of the unfiltered Sr data for the three adult *Nemadactylus macropterus* of Figure 3, at lags (intervals between points correlated) of 0 to 10 points. The correlations become insignificant ($P>0.05$) at lags of 4 to 6 points, varying slightly among specimens. Points are spaced 25 µm center-to-center.

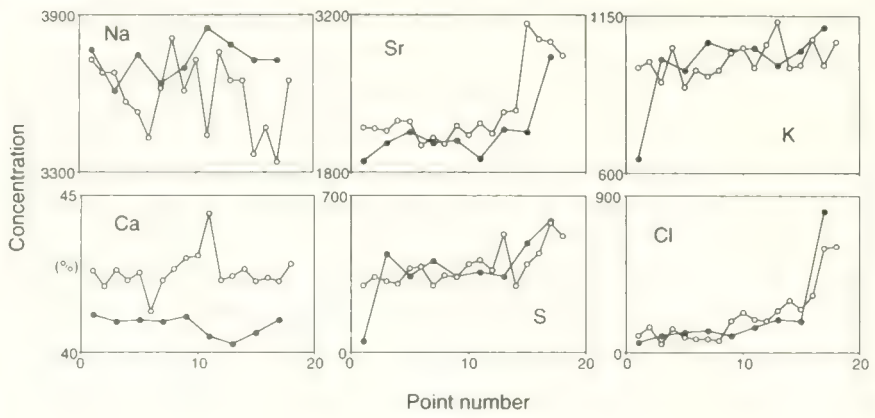


Figure 6

Comparison of parallel fine-scale (open circle) and coarse-scale (solid circle) transects of the outer margin of an adult *Nemadactylus macropterus* sagitta. Distance between the parallel scans was approximately 20 μm. Fine-scale analysis was done with a 6-μm diameter beam at 8-μm intervals, center to center, and with a beam-power density of 2.92 $\mu W \cdot \mu m^{-2}$; coarse-scale analysis was done with a 14-μm beam at 16-μm intervals and with a beam-power density of 2.44 $\mu W \cdot \mu m^{-2}$. Concentrations are reported in units of ppm by weight for all elements other than Ca, which is reported as percent by weight. The large disparity between the two analyses in Na and Ca concentrations is an expected consequence of the different beam-power densities used in the two runs (see Gunn et al., 1992).

variation in the three specimens depicted range up to 45.4 for Sr, 43.4 for Cl, and 31.3 for S (as opposed to, at the other extreme, 1.8 for Ca). Fourth, ontogenetic patterns in the variation are often consistent across specimens. All *N. macropterus* that we have analyzed, for example, show steep gradients in Sr levels in the region immediately around the primordium. Similarly consistent, though less pronounced, patterns are evident in Na and Ca.

The quality of these data were assessed by comparing life history scans from the left and right otoliths from the same fish. The quality of the match within each otolith pair differs markedly (Fig. 7). The comparisons suggest two principal sources of error. First, there is consistent evidence of the difficulty of tracking identical growth trajectories even within a pair of otoliths from the same individual. In all three pairs, the match between left and right otoliths deteriorates as the otolith margin is approached. We attribute this to the decline in the growth rate of the otolith with age, a corresponding compression of ontogenetic variability and, therefore, a larger effect of errors in tracking through the growth axis on the apparent ontogenetic pattern of composition. Slight differences in the shape of the otoliths also give rise to differences in the length of each section, and hence the spacing of scan points relative to the distance along the growth axis. Most of the left and right differences in specimens #304 and #312 appear to result from these tracking errors; that is, the same ontogenetic patterns and mean concentrations are generally evident but variously expanded or compressed along the growth axis. Second, in four of the six elements examined (Na, K, S, and Cl), mean concentrations occasionally differ between left and right otoliths over relatively large portions of the otoliths. This second source of error is difficult to assess. The mismatch is most evident for Cl in #339 and S in #312, where the scale of the mismatch greatly exceeds machine-induced measurement error. The pattern of the mismatch varies widely and inconsistently among the samples: for example, Cl levels match well in #304, match intermittently and poorly in #312, and differ markedly near the margin of #339, whereas S matches well in #304 and #339 but very poorly in #312. Comparisons of parallel life history scans across a single otolith (e.g. Fig. 6) suggest that differences between otolith pairs of the magnitude observed cannot easily be attributed to either measurement error or slight differences between otoliths in the position of the scan line relative to the main growth axis. We conclude, therefore, that the differ-

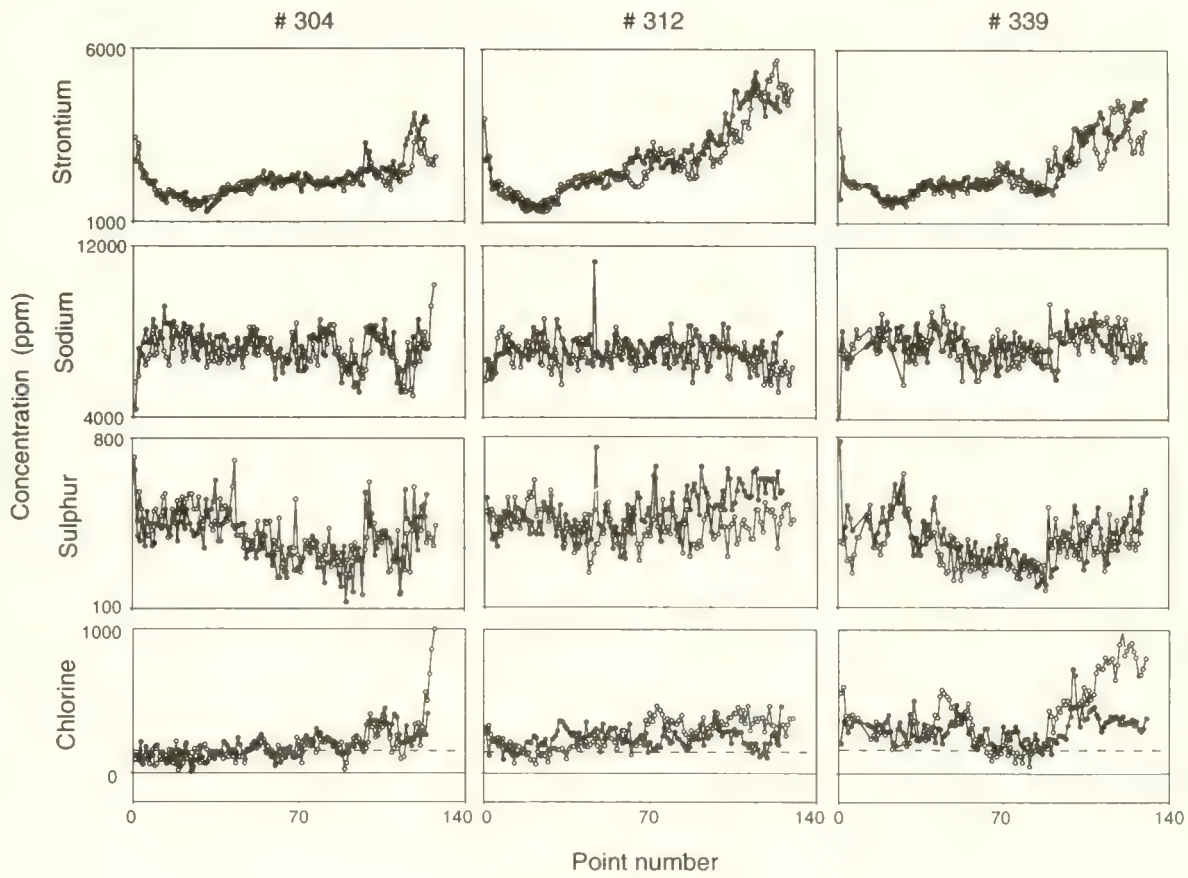


Figure 7

Comparisons of life history transects of the left and right sagittae of three adult *Nemadactylus macropterus* based on unfiltered data for four representative elements (Sr, Na, S, and Cl). The dashed horizontal line in the Cl plots is the minimum detection limit for the element. The comparison is based on identical analytical conditions and an attempt to track as closely as possible the same growth axis in the two otoliths in each pair.

ences between otolith pairs are real, appear to be more common in some elements than in others (e.g. evident in Cl, but not in Sr), and may be more common near the otolith margin than closer to the primordium. The data are limited but clearly indicate that slight differences in elemental concentrations, particularly Cl and S, should be used with caution for stock delineation.

Evaluation of stock structure

We hypothesized that stocks of *N. macropterus* would differ in either or both spawning grounds or times and that these differences would result in diagnostic patterns of composition in the first forming part of the otolith. However, in practice, compositional data for the primordium itself proved of low quality because of the specimen preparation required for EPMA and the incremental structure of otoliths. In most specimens, minute cracks or a pit several microns in diameter developed at the primordium during preparation, the latter because of the 'plucking' of the primordium from the otolith center during polishing. Our previous work (Gunn et al., 1992) indicated that topographic irregularities degrade EPMA data because of unpredictable patterns of x-ray absorption. A comparison of data for point 1 (on and immediately around the primordium) and point 2 (25 µm from the primordium) for the adults supports this conclusion: for all elements except Cl the variance in estimated concentrations is 36 (Na) to 270 % (S) higher for point 1 than for point 2 (Fig. 8). Nevertheless, for all elements, concentrations at point 1 are significantly correlated with those at point

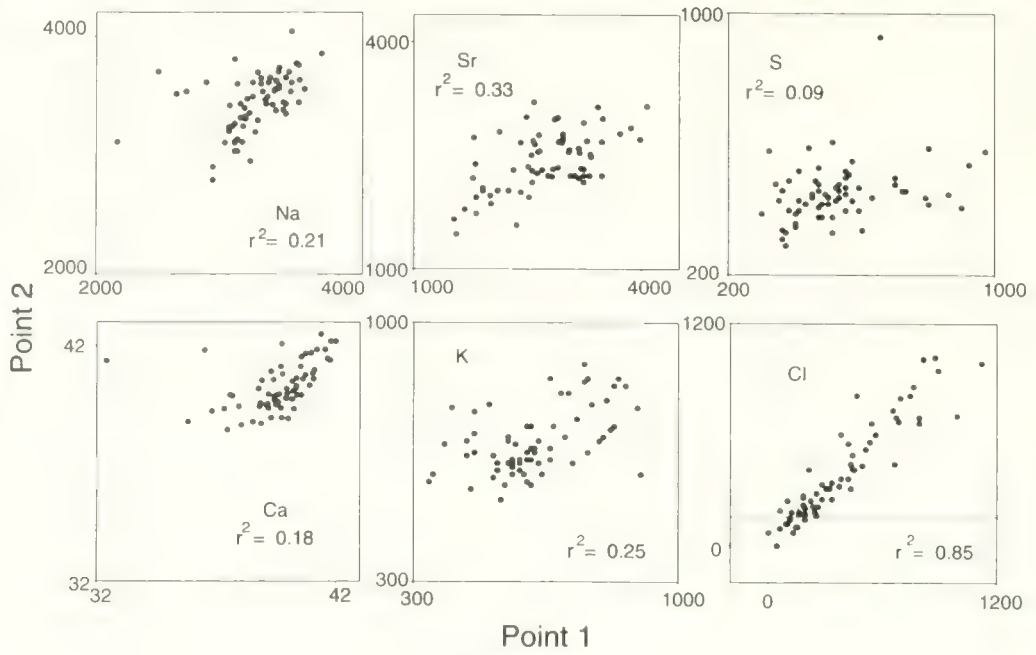


Figure 8

Scattergrams of the relationship between concentrations of the six detected elements (Ca, Na, Sr, K, S, and Cl) as measured on the otolith primordium (point 1) and as measured at a point 25 μm from the primordium (point 2) along the long growth axis of 64 adult *Nemadactylus macropterus*. Concentrations are reported in units of ppm by weight for all elements other than Ca, which is reported as percent by weight. Correlations between the two estimated concentrations are significant for all elements. The slope of the regressions differ significantly from 1.0 for all elements except Cl, although for several elements (Na, K, and Ca) the trend line is very close to a slope of 1 and the calculated regression shifted mainly because of relatively few very low values at point 1. The latter are expected consequences of pitting and cracking on the primordium. Dashed lines in the Cl scattergram indicate minimum detection limits.

2 (r^2 values from 0.09 (S) to 0.85 (Cl)). Slopes for regressions between point 1 and point 2 data are typically not equal to 1, which for most elements probably reflects the highly proteinaceous nature of the primordium. Nonetheless, we conclude that differences among specimens evident in the primordium are also evident adjacent to the primordium, where they can be measured more precisely.

The distributions of mean concentrations of the six elements for the 68 adult *N. macropterus* analyzed are depicted in Figure 9. Three of the six (K, S, and Cl) are significantly skewed to higher concentrations. Ca also shows evidence of a weak skew, and Sr evidence of a weak bimodality. Mean concentrations of four of the six elements differ significantly among sites (Fig. 10), the exceptions being Sr and S. The differences are manifest in both the point 2 and point 2–6 data and are of similar pattern and comparable magnitude in both data sets. For most elements, error bars are smaller in the filtered data, which presumably reflects the reduced effect of random measurement errors. Differences among sites are greatest for Cl: the mean values for three sites (eastern and western Tasmania and the Great Australian Bight) do not differ significantly from the minimum detection limit (MDL), whereas means for the Victorian and New South Wales (NSW) samples are well above the MDL and do not differ significantly from each other. There are suggestions of a similar, though less pronounced grouping of sites in Na and K (concentrations in the Victorian and NSW fish higher than in those from Tasmania and the Bight) and Ca (lower concentrations in Victorian and NSW adults).

The grouping of sites was examined further by plotting Na/Cl and Sr/Ca ratios for specimens from each of the six sites (Fig. 11). These ratios were chosen on the basis of a preliminary survey of the data as likely to separate sites. As expected, the scatter of points

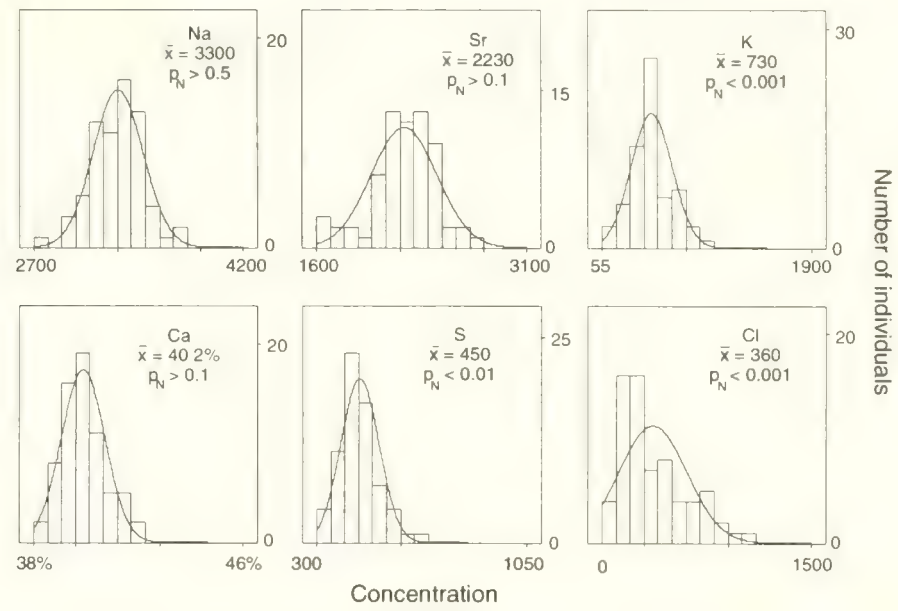


Figure 9

Frequency distributions of concentrations of the six detected elements (Ca, Na, Sr, K, S, and Cl) at point 2 for 64 adult *Nemadactylus macropterus* pooled across sites in SE Australia. P_N=probability the distribution is normal. Concentrations are reported in units of ppm by weight for all elements other than Ca, which is reported as percent by weight.

for individual fish is greater for the single-point data than for the filtered data, but the patterns of regional groupings and the relationships between the concentrations of elements are much the same for the two data sets. Victorian and NSW samples appear to group based on both Na/Cl and Sr/Ca ratios. The two Tasmanian samples group with specimens from the Bight on the basis of Na/Cl ratios but appear to differ based on mean Sr/Ca ratios.

Linear discriminant function analysis (LDFA), for a 3-group discrimination, produces similar results for both single-point and filtered data. For both data sets, the three groups are statistically separable but at a relatively low rate of successful classifications. For the single-point data, 66% of individuals were accurately classified into their three respective 'source populations'; for the filtered data, the success rate increases to 78%. The relatively poor separation is due, in part, to an overlap of the three groups in discriminant space and, in part, to a few individuals located in discriminant space well outside the areas defined by most individuals collected at the same place and time.

For the filtered data, discriminant analysis developed five discriminant functions to classify the six sites. However, only the first three are significant ($P<0.05$), and of these there is a large difference between the first two functions (both at $P<0.01$) and the third ($P=0.02$). Examination of the canonical loadings indicates that discriminant function 1 is correlated with Na, K, and Cl concentrations, and hence represents mainly the initial separation of sites along the Na/Cl axis indicated in Figure 11. The second discriminant function loads heavily only on Sr, whereas the third is mainly a K residual from the first discriminant function. Step-down procedures, in which sites are sequentially pooled, raises the contribution of Ca to the second discriminant function, identifying it with the Sr/Ca axis in Figure 11. The nature of the site separations is indicated in Figure 13. Function 1 separates the two Tasmanian and the Bight (GAB) samples from the two Victorian and the NSW samples; function 2 distinguishes weakly between the GAB sample and the remainder; and function 3 separates the east and west coast Tasmanian samples. The remaining two functions do not clearly distinguish among any sites. The primacy of the first three functions remains in a step-down procedure, as the sites are sequentially pooled based on their degree of overlap. The final step, at which all func-

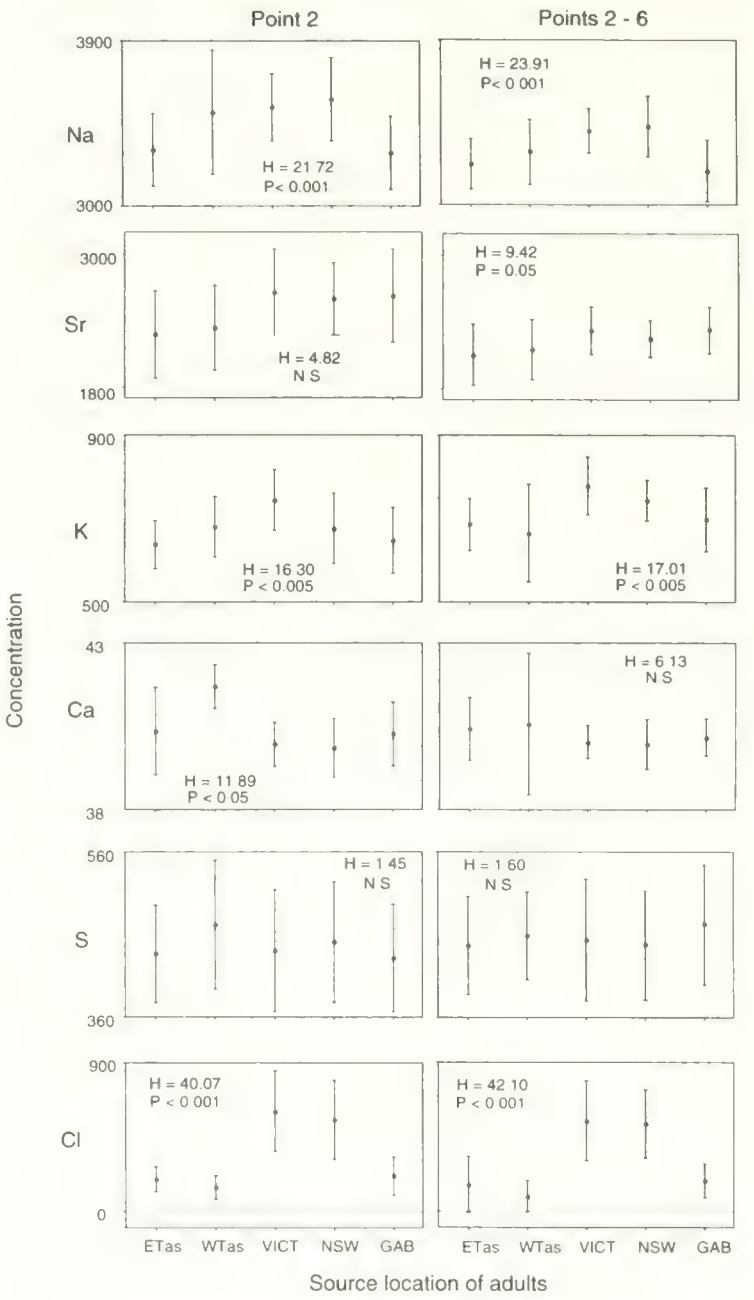


Figure 10

Differences among the six adult *Nemadactylus macropterus* sampling sites in the estimated concentrations (means and standard errors) of the six elements detected by EPMA (Ca, Na, Sr, K, S, and Cl), based on point 2 only and on the mean of points 2–6 inclusive for each individual examined. Concentrations are reported in units of ppm by weight for all elements other than Ca, which is reported as percent by weight. The two Victorian samples were pooled for this comparison. Site labels are defined in Figure 1 and Table 1.

tions contribute significantly ($P<0.001$) to the discrimination, is at the level of three groups and two discriminant functions (i.e. Fig. 12); the third function, separating the two Tasmanian samples, is not quite significant in the final step ($P=0.057$). Post-hoc analyses (Steffe's F-test) of the discriminant functions indicate that the samples from the Victorian and NSW sites do not differ significantly and consistently in any of the three functions, the GAB sample differs from all other sites (which do not differ significantly) in function 2, and none of the sites differs significantly in function 3, though the western Tasmanian sample nearly differs significantly from the other sites.

We draw three general conclusions from these analyses. First, there are significant differences among samples from different sites in terms of the composition of the primordial region of their otoliths. Second, analyses of the primordium itself, of a point 25 µm from the primordium, and of the mean value for the region between 25 and 125 µm from the primordium produce similar results, indicating that distributional differences of adults are manifest through at least the first 125 µm of otolith growth. And third, on the basis of common patterns of composition, the sites pool into three groups: one composed of the NSW and the two Victorian samples, a second consisting uniquely of the Bight sample, and a third consisting of the two Tasmanian samples. In both cases where sites are pooled, the pooled sites are geographically contiguous and nearest neighbors.

Site-specific differences and similarities in ontogenetic variation in composition

That differences in composition among sites can be discerned at points as far out as 125 µm from the primordium and to an apparent age of 45–55 days post-hatching suggest that delineation among samples is not a function of conditions specific to the spawning sites. Any environmental differences must encompass at least several weeks, perhaps months, of larval development. To assess the ontogenetic patterning of these chemical differences, we compared the concentrations of apparent key elements for specimens from the three pooled areas (NSW/Victoria, the Bight, and both Tasmanian sites) at several points along their respective long growth axes. Five-point filtered data were assessed at four positions: points 2–6, 6–10, 36–40, and 80–84. The first position is immediately adjacent to the primordium; the second immediately exterior to the first (and presumably encompassing the second 2–3 months of planktonic larval development); the third we estimate to correspond approximately to the age when the prejuveniles recruit to the nursery areas; and the fourth, outermost position, is the farthest along the growth axis at which we had data for all specimens (the number of points depended upon the length of the axis) and, we estimate, corresponds to otolith deposition at an age of 2–3 years.

The results of the comparison (Fig. 14) lead to three conclusions. First, the mean pattern of ontogenetic change in composition is very similar for samples from all three pooled sets of sites, e.g. Na and Sr concentrations decline between points 2 and 6 and

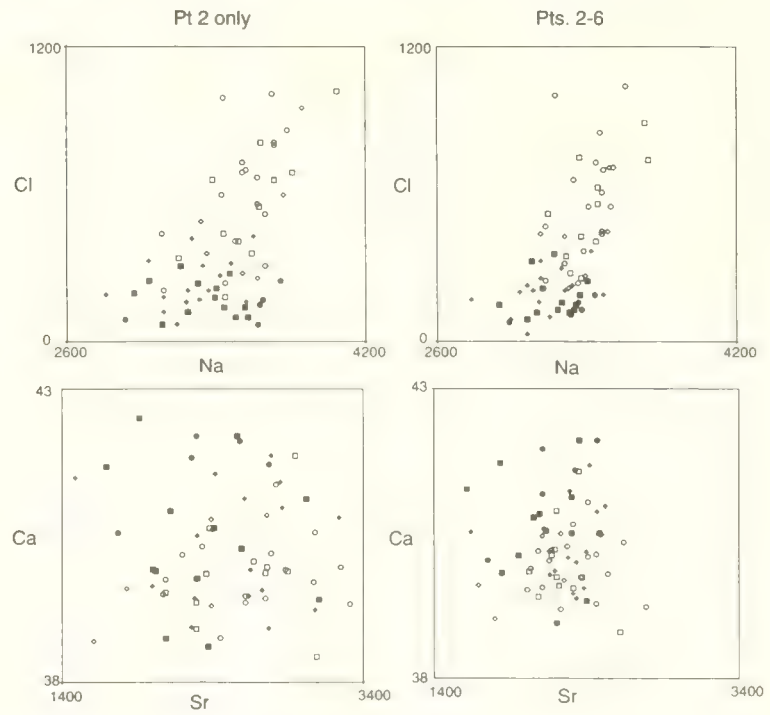


Figure 11

Scattergrams of the relationships between Na and Cl and between Sr and Ca concentrations among the 64 adult *Nemadactylus macropterus* examined, grouped by site, based on concentrations measured at point 2 only and the mean concentration for points 2–6, inclusive. Concentrations are reported in units of ppm by weight for all elements other than Ca, which is reported as percent by weight. Sites are described in Figure 1 and Table 1. Site key: E. Tas.=solid square; W. Tas.=solid circle; NSW=open square; E. Vict.=open circle; GAB= plus sign; and W. Vict.=open diamond.

then increase towards the otolith margin in samples from all three sites. Second, the pattern of ontogenetic variation in concentrations differs among elements. And third, similar mean differences are evident among sites irrespective of where the analysis was done in the otolith. NSW/Victorian specimens, for example, at all stages of their life histories to an apparent age of at least 2–3 years tend to have Cl levels higher than those of fish collected elsewhere. As a result, discriminant analyses based on mean concentrations at points 36 and 80 result in site delineations virtually identical to those derived from concentrations measured near the primordium.

Evaluation of signatures specific to nursery areas and the links between nursery areas and adult groups

The links between nursery areas and spatial components of the adult populations can be assessed in two complementary ways: 1) by determining the source affinities (e.g. spawning site) of juveniles collected in each nursery area and 2) by developing a specific

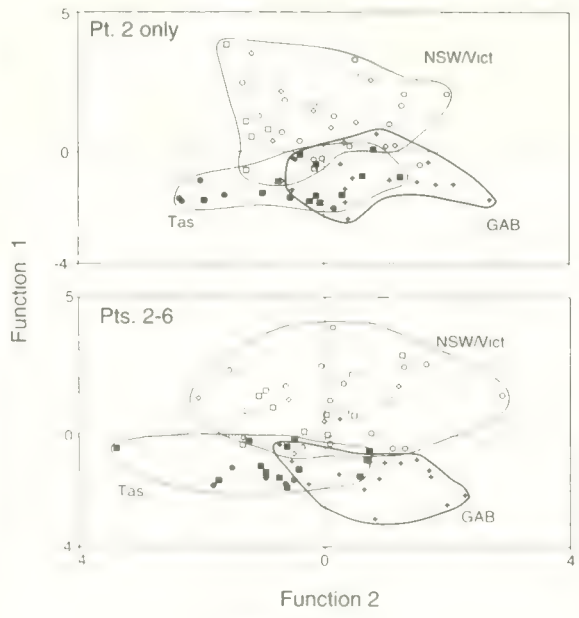


Figure 12

Distribution of adults from each of the six sampled sites (see Fig. 11 for key) in two-function space as determined by a three-group linear discriminant function analysis based on point 2 data and the mean concentrations for points 2–6 inclusive of the six detected elements for each individual. Outlines around each group were drawn by eye. Differences among groups are significant at $P<0.001$ in both analyses (for point 2 only, $F_{12,120}=6.21$, Wilk's lambda=0.35; for filtered data, $F_{12,120}=8.72$, Wilk's lambda=0.29).

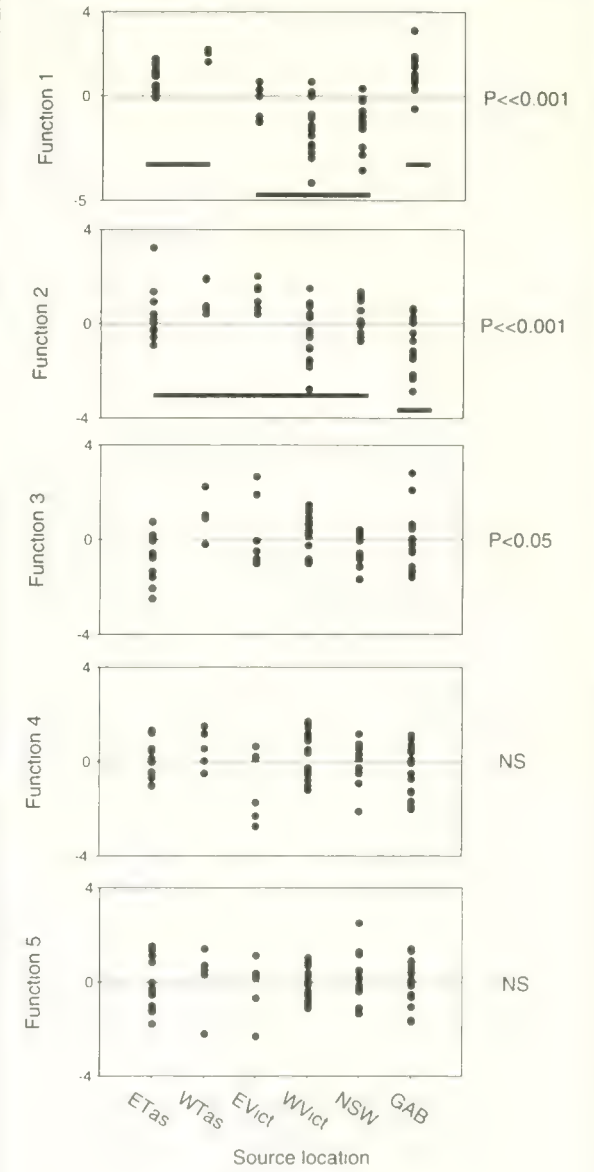
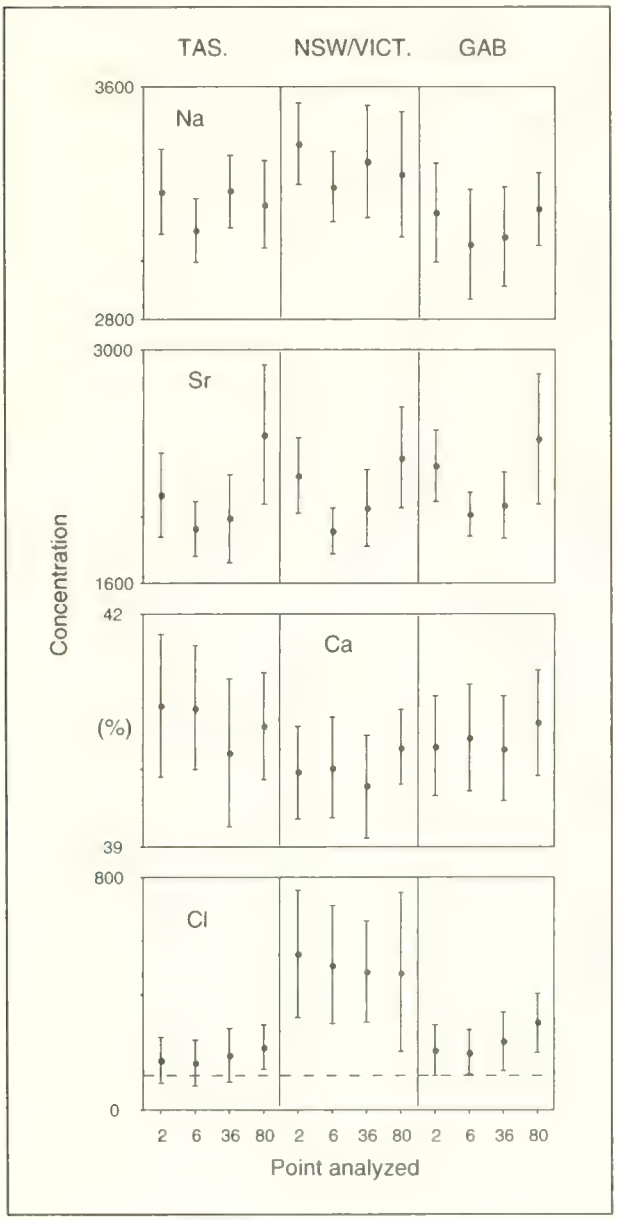


Figure 13

Distribution among sites (see Fig. 1) of values of each of the five discriminant functions defined by the initial (six-site) discriminant function analysis for adult *Nemadactylus macropterus*, based on mean concentrations for points 2–6, inclusive. Horizontal bars indicate sites that pool together based on post-hoc analysis (Steffe's *F*-test). In the case of Function 3, the overall ANOVA is just significant at $P<0.05$, but pairwise comparisons among sites indicate no single or set of sites that differs consistently and significantly from the others. NS=not significant.

signature for each nursery area (based on otolith material deposited during residence in the nursery areas) and using these to classify adults collected in different regions. In essence, the former assesses how juveniles from each of the putative populations are distributed among nursery areas, whereas the latter assesses the contribution of each nursery area to adults collected at each site. With specific regard to *N. macropterus*, if SE Tasmania is the sole nursery area for the species in Australia, then we would expect that 1) the complete range of chemical patterns documented in the adults, at all sites sampled, would be seen in juveniles collected in the single, common nursery area, and 2) adults collected at all sample sites would have a nursery area 'fingerprint' similar to that of the juveniles collected.



For the first analysis, the three-site discriminant functions developed from the adults were used as a training set to classify each of 116 recently settled *N. macropterus*. The data for the juveniles were acquired in the same way as for the adults. Analysis is based on the mean values for points 2–6 from the primordium. Most juveniles were collected in SE Tasmania; a small number were also collected at Phillip Island, Victoria (Table 1).

Most juveniles examined fell within or close to the areas in discriminant function space defined by the adult groups (Fig. 15); only one, with an exceptionally high value on the function 2 axis, did not match the characteristics of at least one of the three adult groups. Moreover, most juveniles classified with the adults collected in the same area. Of the 106 juveniles caught in Tasmania, all but 25 classified with the Tasmanian adult samples, and of these, 13 classified ambiguously, with a probability >25% of being Tasmanian. Overall, only 7% of the Tasmanian-collected juveniles had a probability of <10% of classifying with the Tasmanian-caught adults (Fig. 16). Samples from the five Tasmanian sites were distributed similarly in two-function space (Fig. 15), though the variance was conspicuously higher at one site (Cygnet).

The pattern was similar for juveniles collected off Victoria (Phillip Island), although sample sizes were too small to draw strong inferences. Of the 10 individuals examined, six classified with the NSW/Victorian adults, three classified with the Tasmanian-caught adults (at probabilities ranging from 72 to 85%), and one classified with the Bight-caught adults (at P=63%). The probability that the Victorian juveniles classify with the NSW/Victorian adults is markedly bimodal (Fig. 16) with peaks at >95% and between 5–10%. That is, most individuals had either a very high or very low probability of classifying with the local adults. A similar pattern may also be the

Figure 14

Comparisons of mean concentrations of four elements (Ca, Na, Sr, and Cl) at four points along the life history scan of each adult *Nemadactylus macropterus* pooled by groups identified by linear discriminant function analysis (LDFA). For each individual and point, data were calculated as the mean of the 5-point moving average, beginning at the point indicated (i.e. 2=mean of points 2–6, inclusive; 6=mean of points 6–10, inclusive, etc.). K and S are not depicted as the former generally varies similarly to Na, whereas the latter did not differ significantly among groups. Horizontal dashed line in Cl plot indicates minimum detection limit. Vertical lines about each mean indicate one standard error of the mean. Concentrations are reported in units of ppm by weight for all elements other than Ca, which is reported as percent by weight.

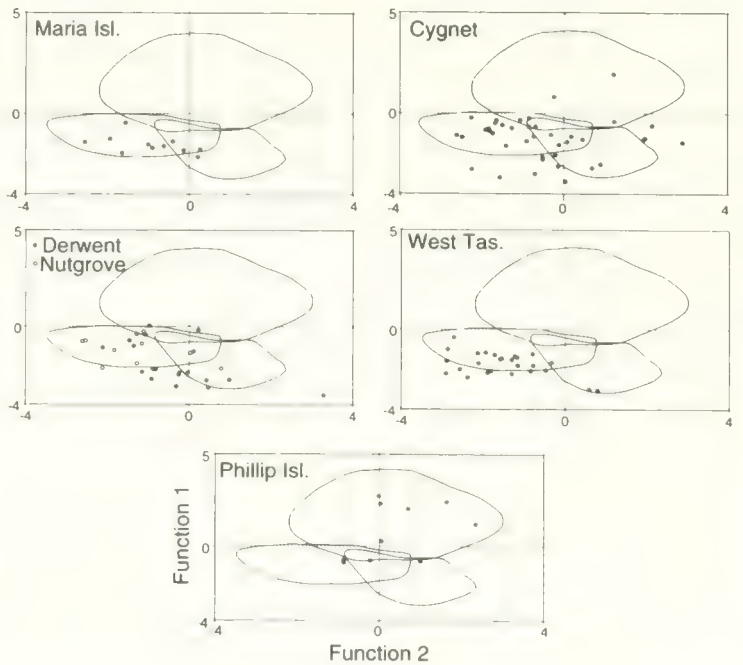


Figure 15

Distribution of individual juvenile *Nemadactylus macropterus* from each of the six sampling sites (see Fig. 1 and Table 1) in two-function space as defined by the three-group LDFA of the adults, based on mean concentrations of the six detected elements at points 2–6, inclusive. Circles enclose areas in two-function space defined by the three adult groups (see Fig. 12).

case among the Tasmanian-caught juveniles. There is an indication of modes at either end of the probability spectrum and possibly a third mode centered near 35%.

The second analysis of the link between nursery areas and the adult population requires analysis of that portion of the otolith deposited while the individuals were in the nursery areas. The otolith of the smallest juvenile we found had a longest growth axis (posterior to primordium) 500 µm in length; several other small fish had similar growth axes in the range of 570–650 µm. Therefore, we examined a standard region approximately 600–800 µm posterior to the primordium along the main growth axis as otolith deposited early in the nursery area stage of development. Specifically, we used as the datum of interest for

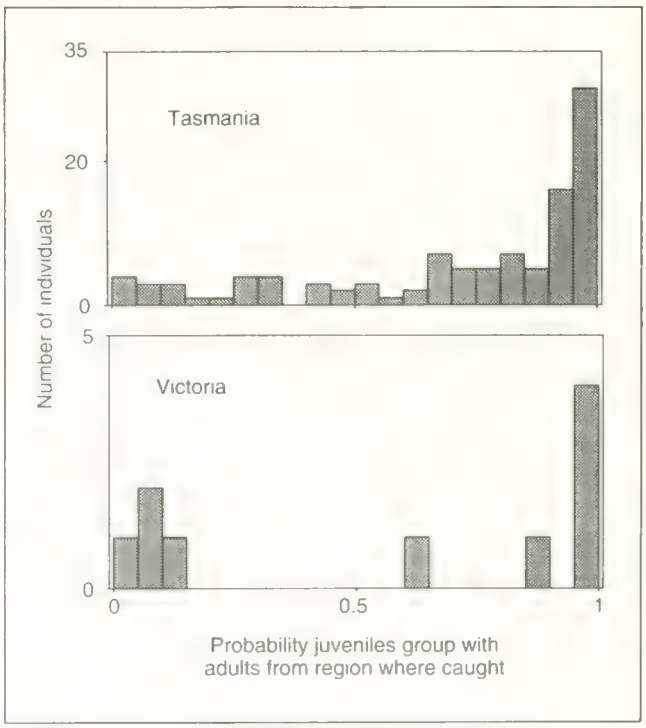


Figure 16

Distribution of probabilities that juvenile *Nemadactylus macropterus* caught in each of the two regions sampled (Tasmania and Victoria) group with adult samples collected in the same regions as defined by the three group LDFA of the adults.

each specimen the mean composition of points 35–39, inclusive, in a standard life history scan (680 to 780 µm from the primordium). All juveniles used in these analyses had otoliths at least this large.

Discriminant analysis of the juveniles indicated highly significant differences among all six areas sampled. The weakest discriminator (the fifth root of the discriminant analysis) was significant at $P<0.01$. The preliminary conclusion then is that there are signatures specific to each nursery-area that could be sought in the adult population.

Further analyses of the data, however, indicated this conclusion was premature. Specifically, if there are nursery-area-specific environmental signals in the otolith, then we would expect them to be manifest ontogenetically in either or both of two ways. First, we would expect that at the end of the larval period (approximately points 25–30), the mean concentrations of various elements would diverge among sites, reflecting the specific environment at each (i.e. the nursery area 'fingerprint'). Second, we would also expect that among individuals, concentrations of these same elements would converge within sites, reflecting recruitment into a common environment. Again, this convergence should occur at approximately points 25–30. For the second prediction, we analyzed in detail one site (Cygnet) for which the sample size of juveniles was large enough that we could reduce possible variability due to differences in date of recruitment. This was done by examining juveniles caught on the same day and falling within a narrow size range (7–11 cm SL).

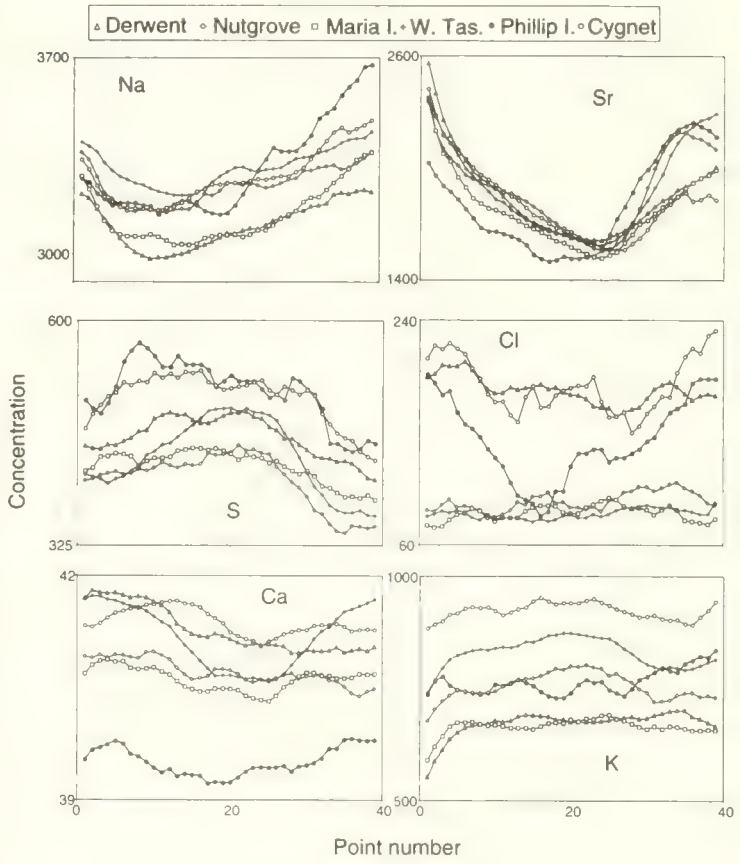


Figure 17

Group mean concentrations of each of the six detected elements (Ca, Na, Sr, K, S, and Cl) for the interior-most 40 points analyzed along the long growth axis of sagittae of juvenile *Nemadactylus macropterus* caught at each of the six nursery areas sampled (see Fig. 1 and Table 1). Point 1 is on the primordium. Data for each individual were filtered through a five-point moving average before the group mean was calculated.

For most elements (all but Sr), neither prediction is supported by the data (Figs. 17 and 18). Although variance is high at all points, there is little or no indication of either divergence among sites (in the case of mean concentrations) or convergence among individuals (in the case of variation within the single site) at or near points 25–30 for any element other than Sr. For Sr, however, both predictions appear to be borne out. Mean concentrations overlap broadly among juveniles from all sites during the larval stage but diverge significantly among sites at about point 25. Among individuals, juveniles at Cygnet appear to converge on two different postrecruitment Sr trajectories, also beginning at about point 25. The available evidence suggests that concentrations of elements other than Sr are largely unaffected by the transition from the larval to the juvenile stages and that the apparent discrimination among nursery-areas is the manifestation of differences among individuals already evident in their larval stages.

We tested this conclusion by reanalyzing for "nursery-area-specific signals" using data for points 2–6 (early larval life) rather than for points 35–39 (early juvenile stage). In general, the results were similar to those obtained with points 35–39, with good discrimination among most nursery grounds and a comparable level of overall site separation (Wilk's lambda=0.20 for points 2–6 vs. 0.22 for points 35–39, $P<0.001$ in both cases). However, the accuracy of correctly assigning juveniles to nursery areas was less in the point 2–6 analysis (51% vs. 82%), which reflects the divergence of Sr concentrations in the nursery areas and its increased importance as a discrimi-

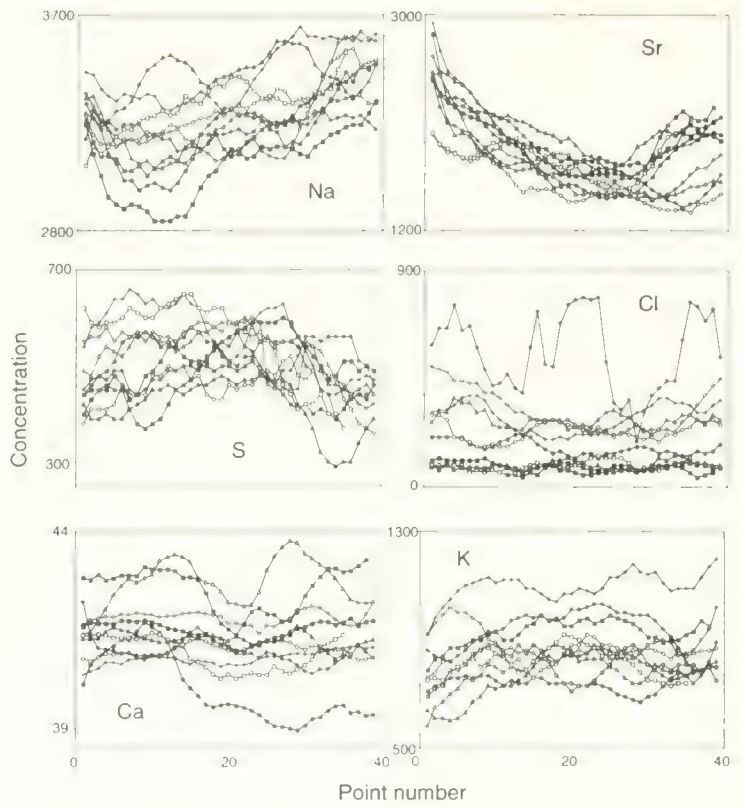


Figure 18

Individual life history trajectories (interior-most 40 points) for each of the six elements (Ca, Na, Sr, K, S, and Cl) detected in the sagittae of juvenile *Nemadactylus macropterus* collected at Cygnet (SE Tasmania). To minimize potentially confounding effects of variation in date of settlement, the comparison was restricted to juveniles collected on the same day (19 December 1987) and in the same size range (7–11 cm standard length). The data for each individual have been filtered through a five-point moving average.

nator. Two discriminant functions (2 and 3) load onto Sr at $r>0.5$ in the original analysis, whereas Sr does not achieve this load level for any function in the point 2–6 analysis. Reflecting this, mean Sr concentrations differ among nursery areas at $P<0.001$ ($F_{5,110}=6.21$) in the original analysis, but at only $P<0.02$ ($F_{5,110}=2.82$) for the point 2–6 analysis. By comparison, differences among nursery areas for the other five elements are significant at similar levels for the two analyses.

Discussion

Effects of data quality on stock delineation

Electron-probe microanalysis with WD-spectrometers revealed extensive variability in the concentrations of six elements in *N. macropterus* otoliths. Some of this variability is induced by the inherent, small-scale compositional heterogeneity of otoliths and some is noise that reflects the limits of detectability and precision of the electron probe. However, comparisons of life history scans along similar growth axes of left and right otolith pairs indicate significant ontogenetic variability for all elements. For most elements, there is also evidence of geographic variability in composition.

The extent to which this ontogenetic and geographic variability can be used to detect differences in either life histories or population structure critically depends on the scale of the life history or population 'signal' relative to analytical 'noise.' In that regard, data quality varies widely among elements. Two identifiable sources of this 'error' are the effects

of beam conditions, which differ among elements (e.g. Na analysis was more sensitive to effects of pitting than was analysis of Sr) (see Gunn et al., 1992), and the low precision of estimates for elements at low mean concentrations (e.g. Cl and S). The effects of these factors can be estimated from standard formulae and empirically by comparing 'replicate' analyses on the same otolith. In practice, true replication is impossible, owing to the effects of beam damage and small-scale heterogeneity in composition, but it can be approximated by comparing points in two parallel life history scans. Our comparison (Fig. 6) is also a worst-case scenario in that it also includes the effects of different beam-power densities and point spacing in the two scans, which can be expected to have a marked effect on the estimated concentrations of some elements, such as Ca. Nonetheless, for the five elements other than Ca, differences between 'replicate points' are still on the order of the theoretical analytical precision (Table 2) and suggest a conservative difference criterion between point analyses that ranges from 331 ppm for Sr to 73 ppm for Cl (Table 2).

Ontogenetic comparisons also require that otolith sections be accurately duplicated among individuals. Our test of this accuracy—a comparison of left and right otoliths from single individuals—leads to three conclusions. First, despite our best efforts we could not guarantee duplication of the life history track between otoliths. Pairwise comparisons suggest variable compression and expansion of the ontogenetic signal between pairs, which presumably reflects slight differences between otoliths in the beam path relative to the main growth axis. The accuracy of duplication was generally high, but also differed among individuals and declined as distance from the primordium increased. Second, nonetheless, the overall pattern of peaks and troughs in the pairs of otoliths compared was generally quite similar. As a result, the principal ontogenetic patterns in, for example, Sr concentrations would be reflected in both otoliths, but examination of one alone could lead to erroneous conclusions about the life history stage at which a particular change in concentration occurred. The variability in life history scans induced by differential compression renders statistical comparisons of ontogenetic patterns extremely difficult and liable to subjective interpretation. In theory, these difficulties could be overcome by calibrating ontogenetic changes in composition against real age—as opposed to distance along the growth axis—but difficulties in resolving the ages of larger individuals are likely to make this approach problematic for most species.

Third, for at least some elements, mean concentrations and ontogenetic patterns appear to differ between otoliths even within the same individual. In two of the three pairs examined, mean Cl and S concentrations differed significantly between otoliths over relatively large sections of the main growth axis and at levels well above measurement error. This asymmetry was so surprising that we repolished and reanalyzed one pair of otoliths (specimen #312) to confirm the results; the second series of data were virtually identical to the first. The implication is that otolith pairs do not encode life history information in the same way. As yet, sample sizes for this comparison are much too small to assess the generality of mismatches and the scale of the problem, but the available information suggests treating with caution data obtained from single point analyses in otoliths.

Another potential source of methodological errors is specimen contamination. J. Calaprice (in press), for example, discounted Cl as a stock discriminator in his studies on Atlantic bluefin tuna, *Thunnus thynnus,* because the element is widely present in the laboratory environment and easily transferred during specimen preparation and handling. Given this, the dependence of our site separation on variation in Cl concentrations is of concern. Although contamination is a critical issue (particularly at the sub-ppm level), several of our observations are not immediately consistent with the contamination hypothesis. First, Cl does not vary independently; its concentrations in otoliths covaries among specimens with Na and K. If Cl concentrations are principally contaminants, the same contamination must affect Na and K concentrations, which is unlikely. Second, samples collected in the same region but at different times, different places, and with different gear types (e.g. juveniles and adults from the Tasmanian sites collected by hook-and-line and trawling) exhibit similar concentrations of Cl, suggesting that observed variability is not a consequence of the way individuals are caught and handled. And third, the order in which the specimens were prepared and analyzed was randomized to check for systematic error; none was detected.

Evidence for regional variation in otolith composition

Several previous studies, using probe microanalysis (e.g. Radtke, 1989; Kalish, 1990) and whole otolith analysis (e.g. Gaudie et al., 1986; Edmonds et al., 1991), have demonstrated that otoliths vary in composition ontogenetically and regionally. Our data permit a detailed evaluation of the interaction between these components of variability. However, because we could not collect and analyze otoliths of larvae from known spawning areas our results only test

indirectly the potential of the technique to resolve spawning stock structure. Specifically, we sought evidence of regionally different patterns in otolith composition that might reflect stock structure.

In that regard, concentrations measured near the primordium differed significantly for four of six elements among adults from the six sites. In all four cases, the range of mean values among sites exceeded an empirically derived 'minimum significant difference' by at least 50% (Table 2). Furthermore, the pattern of differences among sites appeared to be regionally based: the two Tasmanian samples pooled together in the discriminant analysis, as did the geographically contiguous NSW and Victorian samples. Such a grouping of sites could imply any of four different mechanisms: 1) all sites differ, and the grouping is a statistical artefact of the small number of sites and individuals sampled; 2) regional differences result from retrospective changes in otolith chemistry in response to the latest conditions encountered by each adult, and adjacent sites pool because their environmental characteristics are more similar than those of widely separated sites; 3) the sites pool because each regional set derives uniquely from a common spawning ground or spawning population; and 4) each set is derived from a number of spawning grounds or populations that have similar chemical fingerprints, within which individuals mix widely and the boundaries of which are set by constraints on adult or larval mixing.

The possibility that the regional groupings are an artefact is difficult to evaluate without knowing the range of chemical fingerprints possible and their likelihood of occurrence. Assuming three chemical phenotypes randomly distributed among six individuals (=sites), then the probability that at least two adjacent sites will have identical characteristics is extremely high. However, given the number of possible permutations, the probability that all pooling of sites will be only among nearest neighbors is less than 0.01. Therefore, we reject the hypothesis that the apparent regional groupings are a statistical artefact.

We also think it unlikely that the groupings (and similarity of fish within sites) are the result of retrospective modification of otolith chemistry. It is a consistent assumption of otolith-based aging studies that otolith structure is not modified after deposition. A similar assumption underlies chemical studies, although there are no experimental data to verify the point (as opposed to studies on scales, the chemical compositions of which are modifiable retrospectively, e.g. Sauer and Watabe, 1989). In fact, it is likely that at least some water- and alcohol-soluble compounds are transported into or out of otoliths during preservation. However, our data are not consistent with such retrospective modification of the micro-constituents. *Nemadactylus macropterus* collected at the same site and time show little evidence of convergence on a common marginal composition. This implies that recent environmental history has little or no effect on the composition of the otolith margin and presumably even less on the interior. Where a common marginal composition was evident, as in Sr levels among juveniles collected in the same area, it appears to be related to an environmental effect during deposition rather than to retrospective modification.

Distinguishing between the other two hypotheses—a single spawning ground for each regional phenotype or multiple spawning grounds with regionally restricted mixing—is not possible without additional information. As noted, information on the reproductive biology of Australian *N. macropterus* is sparse. Smith (1989) found running-ripe individuals in autumn (February–March) off NSW; we found large numbers of relatively young larvae present along the east, but not the west, coast of Tasmania (for sampling sites and protocol, see Thresher et al., 1989), and several unpublished reports indicate similar larvae off Victoria and South Australia (in the Bight). These scattered observations suggest that *N. macropterus* spawn at a number of sites along the southeastern Australian coast and certainly spawn in each of the three regional groupings of sites identified by otolith chemical analysis. But sampling is not yet detailed enough to determine whether there are discrete spawning areas, or whether spawning occurs in a continuous band of activity all along the coast. Genetic data provide little additional information. Richardson's (1982) samples were drawn from Tasmanian and NSW/Victorian sites and hence appear to bracket two otolith-based regional groupings but indicate no significant genetic differences across this range. This result has recently been confirmed by Elliott and Ward (1994) for allozymes and Grewe et al. (1994) for mitochondrial DNA.

The lack of genetic differentiation in southeastern Australian *N. macropterus* populations is consistent with our observations of apparent examples of larval mixing. Probe microanalysis of otoliths of juveniles from Victorian and Tasmanian coastal habitats indicated that most are similar in composition to those of adults collected at the same sites, which suggests regional, self-recruiting populations. However, the distribution of the probabilities that each juvenile originated in the region where it was collected was conspicuously bimodal. Four out of ten juveniles caught off Victoria had chemical phenotypes more typical of Tasmanian (3) or Bight (1) origin, whereas 8 of 106 Tasmanian-caught juveniles classified mainly with the NSW/Victorian adult sample.

Although the data are obviously preliminary, these mismatched individuals could be direct evidence of an exchange of individuals among populations during the larval stage. The apparent exchange rate varies depending upon the criterion selected and may well differ with site. Even a conservative estimate for the Tasmanian samples (i.e. defining migrants as individuals with a probability >90% of not being derived from the Tasmanian adults) nonetheless suggests an exchange rate of about 7–8%, which is high enough to prevent genetic divergence among samples from the NSW, Victorian, and Tasmanian sites (Elliott and Ward, 1994).

Determinants of otolith composition

The working hypothesis underlying our approach is that otolith composition is largely determined by environmental factors that presumably differ at relatively fine space scales. The data to support this environmental sensitivity, however, are not abundant and to a large extent are drawn from the invertebrate literature (e.g. Rosenberg, 1980; Schneider and Smith, 1982). Studies on teleosts are ambiguous. To date, all reported effects have involved Sr, which has been reported as sensitive to changes in salinity (Radtke et al., 1988; Kalish, 1990; Secor, 1992) and temperature (Radtke et al., 1990; Townsend et al., 1992; however, see Kalish, 1989; and Gallahar and Kingsford, 1992).

There are two reasons to suspect that most of the elements detected in our study are less responsive to the environment than is widely assumed. First, most are physiologically important and their concentrations tightly regulated in plasma and hence presumably in endolymph (Kalish, 1991). For example, an expectation that relatively slight changes in salinity significantly affect the incorporation of Na and Cl in otoliths is unrealistic in an animal with well-developed osmoregulatory mechanisms. Of the six elements detected, only Sr is likely to be relatively unaffected by such physiological controls, though it is presumably affected by many of the same factors that constrain variation in Ca concentrations and may well be subject to a suite of other physiological constraints (see Kalish, 1991).

Second, our data are not consistent with a strong and direct effect of the environment on composition. Two observations are particularly relevant: 1) settlement into nursery areas had no apparent effect on otolith chemistry, other than a slight effect on Sr, and 2) differences among regional groupings are manifest from the primordium to nearly the otolith margin and hence were apparently unaffected by life history stage, irrespective of habitat occupied. Regarding the transition to the nursery areas, for elements other than Sr there was no indication of convergence on a common chemical phenotype by individuals in a given nursery area, nor evidence of divergence among nursery areas in response to local conditions. This suggests that the concentrations of 5 of the 6 elements we measured do not vary in response to environmental conditions in the nursery areas in any direct way. The nursery areas sampled ranged from mid-shelf to shallow coastal embayments and differed markedly in temperature and salinity histories, water-column chemistry, depth, substratum, turbidity, and in invertebrate composition (and hence presumably in the diets of the juveniles). The apparent lack of an impact of any of these on otolith composition suggests their effects at the >100 ppm level are weak or indirect (or both), except possibly for effects on Sr. Similarly, the consistency of regional differences in concentrations through life suggests these differences are largely unaffected by changes in habitats that range from high seas nekton to coastal embayments. Although the concentrations of several elements (Sr, Na, K, and S) clearly vary ontogenetically in otoliths, this variation is superimposed on, and apparently separate from, whatever determines regional differences in composition.

The causes of the regional 'base' differences in composition are not clear. There are several broad possibilities:

- The chemical phenotype is modified retrospectively, based on the adult habitat or sample preparation; for reasons discussed above, we think this mechanism unlikely;
- Life cycles for each region are closed within areas of a uniquely diagnostic environment. This seems unlikely given the diversity of habitats occupied by the species during its life history, but cannot be rejected until the factors that affect otolith composition are determined;
- The base composition is ontogenetically set by environmental influences early in the larva's life, and then maintained, although overlayed by ontogenetic modification, throughout its subsequent life and environmental history;
- The base composition is determined genetically.

The information currently available is not sufficient to discriminate between a 'locked phenotypic effect' (#3) and a genetic hypothesis (#4). A key datum that would permit such discrimination is a measure of year-class effects on otolith composition. Regional differences in otolith composition that vary among year classes argue against a genetic basis and for an environmental influence early in larval devel-

opment. Our current data are much too sparse for any statistically powerful test of year-class differences, but preliminary results suggest only small differences among years for most sites. This is consistent with the similar classifications of adults and juveniles for both the NSW/Victorian and Tasmanian regional groupings; although the adult and juvenile samples differ in mean birth date by five years (adults from the 1980–84 year classes, juveniles from the 1987 and 1988 year classes), the samples overlap broadly in the concentrations of the regionally diagnostic elements.

We tentatively conclude that the regionally diagnostic 'base' concentrations of most measured elements probably have a genetic basis. This conclusion conflicts with both genetic analyses of the species in Australia (Richardson, 1982; Elliott and Ward, 1994; Grewe et al., 1994), which indicate no regional differences and with our preliminary, conservative estimate of larval mixing among regional groupings. At this point, the data are not adequate to resolve this contradiction. Its resolution, however, critically affects the way compositional data obtained from electron-probe microanalysis are used for stock delineation. If the regional differences are primarily genetically determined, then year-class effects are likely to be relatively unimportant. This simplifies analysis but also implies that the usefulness of the approach depends on the extent and pattern of genetic differentiation among populations. However, if regional differences in 'base' concentrations are primarily determined by environmental effects, perhaps via a 'locked phenotype' mechanism of some kind, then variability among year classes could be a critical covariate in an analysis of population structure. In that case, electron-probe microanalysis is likely to be useful wherever significant environmental differences between spawning grounds are known or suspected.

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Literature cited

Ancey, M., F. Bastenaire, and R. Tixier.
1978. Applications of statistical methods in microanalysis. *In* F. Maurice, L. Meny, and R. Tixier (eds.), Microanalysis and scanning electron microscopy, p. 319–343. Proc. Summer School St. Martin-d'Heres, 1978. Les Éditions de Physique, Orsay, France.

Avise, J. C., C. A. Reeb, and N. C. Saunders.
1987. Geographic population structure and species differences in mitochondrial DNA of mouthbrooding marine catfishes (Ariidae) and demersal spawning toadfishes (Batrachoididae). Evolution 41:991–1002.

Bagenal, T. B., F. J. H. Mackereth, and J. Heron.
1973. The distinction between brown trout and sea trout by the strontium content of their scales. J. Fish. Biol. 5:555–557.

Behrens Yamada, S., T. J. Mulligan, and D. Fournier.
1987. Role of environment and stock on the elemental composition of sockeye salmon (*Oncorhynchus nerka*) vertebrae. Can. J. Fish. Aquat. Sci. 44:1206–1212.

Buchardt, B., and P. Fritz.
1978. Strontium uptake in shell aragonite from the freshwater gastropod *Limnaea stagnalis*. Science 199:291–292.

Calaprice, J. R.
1971. X-ray spectrometric and multivariate analyses of sockeye salmon (*Oncorhynchus nerka*) from different regions. J. Fish. Res. Board Can. 28:369–377.
1985. Chemical variability and stock variation in northern Atlantic bluefin tuna. Collect. Vol. Sci. Pap. ICCAT/ Recl. Doc. Sci. CICTA/ Collecc. Doc. Cient. CICAA 24:222–254.
In press. Applications of X-ray flourescence spectrometry to stock delineation: a historical perspective. *In* R. E. Thresher, J. Ianelli, D. Mills, and C. Proctor (eds.), International workshop on skeletal chemistry of fishes, abstracts and edited transcripts. NOAA Tech. Memo. NMFS.

Calaprice, J. R., H. M. McSheffrey, and L. A. Lapi.
1971. Radioisotope X-ray fluorescence spectrometry in aquatic biology: a review. J. Fish. Res. Board Can. 28: 1583–1594.

Calaprice, J. R., L. A. Lapi, and L. J. Carlsen.
1975. Stock identification using X-ray spectrometry and multivariate techniques. Bull. INPFC 32:81–101.

Cameron, M.
In press. Statistical methods for classification of otoliths. *In* R. E. Thresher, J. Ianelli, D. Mills, and C. Proctor (eds.), International workshop on skeletal chemistry of fishes, abstracts and edited transcripts. NOAA Tech. Memo. NMFS.

Coutant, C. C.
1990. Microchemical analysis of fish hard parts for reconstructing habitat use: practice and promise. Am. Fish. Soc. Symp. 7:574–580.

Edmonds, J. S., M. J. Moran, N. Caputi, and M. Morita.
1989. Trace element analysis of fish sagittae as an aid to stock identification: pink snapper (*Chrysophrys auratus*) in western Australian waters. Can. J. Fish. Aquat. Sci. 46: 50–54.

Edmonds, J. S., N. Caputi, and M. Morita.
1991. Stock discrimination by trace-element analysis of otoliths of orange roughy (*Hoplostethus atlanticus*), a deep-water marine teleost. Aust. J. Mar. Freshwater Res. 42:383–389.

Elliot, N. G., and R. D. Ward.
1994. Enzyme variation in jackass morwong, *Nemadactylus macropterus* (Schneider, 1801) (Teleostei: Cheilodactylidae), from Australian and New Zealand waters. Aust. J. Mar. Freshwater Res. 45:51–67.

Fisheries Agency of Japan.
1967. Study on identification of the Pacific salmon by neutron activation analysis. Survey and Research Division, Fisheries Agency of Japan (cited in Mulligan et al. 1983).

Gallahar, N. K., and M. J. Kingsford.
1992. Patterns of increment width and strontium: calcium ratios in otoliths of juvenile rock blackfish, *Girella elevata* (M.). J. Fish. Biol. 41:749–763.

Gauldie, R. W., D. A. Fournier, D. E. Dunlop, and G. Coote.
1986. Atomic emission and proton microprobe studies of the ion content of otoliths of chinook salmon aimed at recovering the temperature life history of individuals. Comp. Biochem. Physiol. 84A:607–615.

Gauldie, R. W., and A. Nathan.
1977. Iron content of the otoliths of tarakihi (Teleostei: Cheilodactylidae). N. Z. J. Mar. Freshwater Res. 11:179–191.

Grewe, P. M., A. J. Smolenski, and R. D. Ward.
1994. Mitochondrial DNA variation in jackass morwong, *Nemadactylus macropterus* (Teleostei: Cheilodactylidae) from Australian and New Zealand waters. Can. J. Fish Aquat. Sci. 51(5):1101–1109.

Gunn, J. S., I. R. Harrowfield, C. H. Proctor, and R. E. Thresher.
1992. Electron probe microanalysis of fish otoliths—evaluation of techniques for studying age and stock discrimination. J. Exp. Mar. Biol. Ecol. 158:1–36.

Hartl, D. L., and A. G. Clark (eds.)
1989. Principles of population genetics, 2nd ed. Sinauer Associates Inc., Sunderland, MA, 682 p.

Houck, J. E., R. W. Buddemeier, S. V. Smith, and P. J. Jokiel.
1977. The response of coral growth and skeletal strontium to light intensity and water temperature. *In* D. L. Taylor (ed.), Proc. third int. coral reef symp. Miami, Vol.2:425–431.

Kalish, J. M.
1989. Otolith microchemistry: validation of the effects of physiology, age and environment on otolith composition. J. Exp. Mar. Biol. Ecol. 132:151–178.
1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fish. Bull. 88:657–666.
1991. Determinants of otolith chemistry: seasonal variation in the composition of blood plasma, endolymph and otoliths of bearded rock cod *Pseudophycis barbatus*. Mar. Ecol. Prog. Ser. 74:137–159.

Klecka, W. R.
1980. Discriminant analysis. Sage, Beverly Hills, CA, 70 p.

Klokov, V. K., and L. A. Frolenko.
1970. Elementary chemical composition of scales of pink salmon. Izv. Tikhookean. Nauchno-Issled. Instit. Rybn. Khoz. Okeanogr. 71:159–168.

Lapi, L. A., and T. J. Mulligan.
1981. Salmon stock identification using a microanalytic technique to measure elements present in the freshwater growth region of scales. Can. J. Fish. Aquat. Sci. 38:744–751.

Mulligan, T. J., L. Lapi, R. Kieser, S. B. Yamada, and D. L. Duewer.
1983. Salmon stock identification based on elemental composition of vertebrae. Can. J. Fish. Aquat. Sci. 40:215–229.

Mulligan, T. J., F. D. Martin, R. A. Smucker, and D. A. Wright.
1987. A method of stock identification based on the elemental composition of striped bass *Morone saxatilis* (Walbaum) otoliths. J. Exp. Mar. Biol. Ecol. 114:241–248.

Pichou, J. L., and F. Pichoir.
1984. A new model for quantitative x-ray microanalysis. La Recherche Aerospatiale, 3:167–192.

Radtke, R. L.
1989. Strontium-calcium concentration ratios in fish otoliths as environmental indicators. Comp. Biochem. Physiol. 92A:189–193.

Radtke, R. L., R. A. Kinze, and S. D. Folsom.
1988. Age at recruitment of Hawaiian freshwater gobies. Environ. Biol. Fishes. 23:205–213.

Radtke, R. L., D. W. Townsend, S. D. Folsom, and M. A. Morrison.
1990. Strontium:calcium concentration ratios in otoliths of herring larvae as indicators of environmental histories. Environ. Biol. Fish. 27:51–61.

Richardson, B. J.
1982. Geographical distribution of electrophoretically detected protein variation in Australian commercial fishes. II: Jackass morwong, *Cheilodactylus macropterus* Bloch and Schneider. Aust. J. Mar. Freshwater Res. 33:927–931.

Robertson, D. A.
1978. Spawning of tarakihi (Pisces: Cheilodactylidae) in New Zealand waters. N. Z. J. Mar. Freshwater Res 12:277–286.

Rosenberg, G. D.
1980. An ontogenetic approach to the environmental significance of bivalve shell chemistry. *In* D. C. Rhoads and R. A. Lutz (eds.), Skeletal growth of aquatic organisms, p. 133–168. Plenum Press, NY.

Sauer, G. R., and N. Watabe.
1989. Temporal and metal-specific patterns in the accumulation of heavy metals by the scales of *Fundulus heteroclitus*. Aquat. Toxicol. 14:233–248.

Schneider, R. C., S. V. Smith.
1982. Skeletal Sr content and density in *Porites* spp. in relation to environmental factors. Mar. Biol. 66:121–131.

Secor, D. H.
1992. Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass *Morone saxatilis*. Fish. Bull. 90:798–806.

Sie, S. H., and R. E. Thresher.
1992. Micro-PIXE analysis of fish otoliths: methodology and evaluation of first results for stock discrimination. Internat. J. PIXE 2:357–380.

Sinclair, M.
1987. Marine populations: an essay on population regulation and speciation. Univ. Wash. Press, Seattle, WA, 252 p.

Smith, D. C.
1982. Age and growth of jackass morwong (*Nemadactylus macropterus* Bloch & Schneider) in eastern Australian waters. Aust. J. Mar. Freshwater Res. 33:245–253.
1989. The fisheries biology of jackass morwong in eastern Australian waters. Ph.D. thesis, Univ. New South Wales, Australia.

Smith, P. J., A. Jamieson, and A. J. Birley.
1990. Electrophoretic studies and the stock concept in marine teleosts. J. Cons. Int. Explor. Mer 47:231–245.

Smith, S. V., R. C. Buddemeier, R. C. Redalje, and J. E. Houck.
1979. Strontium-calcium thermometry in coral skeletons. Science 204:404–407.

Sokal, R. R., and F. J. Rohlf.
1981. Biometry. Freeman, San Francisco, CA, 859 p.

Thompson, G., and H. D. Livingston.
1970. Strontium and uranium concentrations in aragonite precipitated by some modern corals. Earth Planet. Sci. Lett. 8:439–442.

Thresher, R. E., B. D. Bruce, D. M. Furlani, and J. S. Gunn.
1989. Distribution, advection, and growth of larvae of the southern temperate gadoid, *Macruronus novaezelandiae* (Teleostei: Merlucciidae), in Australian coastal waters. Fish. Bull. 87:29–48.

Tilzey, R. D. J., M. Zann-Schuster, N. L. Klaer, and M. J. Williams.
1990. The south east trawl fishery: biological synopses and catch distributions for seven major commercial fish species. Bureau Rural Resour. Bull. 6, 80 p.

Townsend, D. W., R. L. Radtke, S. Corwin, and D. A. Libby.
1992. Strontium:calcium ratios in juvenile Atlantic herring *Clupea harengus* L. otoliths as a function of water temperature. J. Exp. Mar. Biol. Ecol. 160:131–140.

Vooren, C. M.
1972. Post-larvae and juveniles of tarakihi, (Teleostei: Cheilodactylidae) in New Zealand. N. Z. J. Mar. Freshwater Res. 6:601–618.

Waples, R. S., and R. H. Rosenblatt.
1987. Patterns of larval drift in southern California marine shore fishes inferred from allozyme data. Fish. Bull. 85:1–11.

Weber, N. J.
1973. Incorporation of strontium into reef coral skeletal carbonate. Geochim. Cosmochim. Acta 41: 2173–2190.

Abstract.—The reproductive biology of red drum, *Sciaenops ocellatus*, in the northern Gulf of Mexico is described from examination of 3,351 specimens sampled from March 1986 through September 1992. The sex ratio of the spawning population, as manifest in purse seine collections, was essentially 1:1. Gonosomatic indices and ovarian histology demonstrated an 8-9 week spawning season from mid August to early October. Both sexes achieved >50% maturity at age 4; however, at 50% maturity males were somewhat smaller than females (660–670 mm vs. 690–700 mm, 3.4–3.5 kg vs. 4.0–4.1 kg). Simultaneous observations of oocytes in all stages of maturation throughout the spawning seasons confirmed group-synchronous oocyte maturation and multiple batch spawning. Batch fecundity of 51 females (age 3–33 yr) ranged from 0.16 million to 3.27 million ova per batch (mean=1.54 million ova) and was positively correlated with fork length, gonad-free body weight, eviscerated body weight, and age. Seasonal spawning frequencies estimated from the proportion of mature females with postovulatory follicles varied widely from once every 3 days to once every 80 days. More plausible spawning frequencies (2–4 d) were obtained if proportions of females exhibiting oocyte yolk coalescence and oocyte hydration, indicative of imminent spawning, were included in estimates of this variable.

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Reproductive biology of red drum, *Sciaenops ocellatus*, from the neritic waters of the northern Gulf of Mexico*

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Red drum, *Sciaenops ocellatus* (family: Sciaenidae), has been a prime target species for both recreational and commercial fishermen in the northern Gulf of Mexico. As conflicts over allocation of a purportedly declining population escalated in the mid 1980's, management of the red drum offshore spawning stock became an imperative. However, basic to the formulation of any management strategy is the need for sound biological information, including the various aspects of the species' reproductive biology. Most of the literature on red drum reproduction (see Murphy and Taylor [1990] for a review) has been derived from studies of juveniles and itinerant adults in estuarine waters. Little is known of the reproductive biology of adult "bull" red drum that assemble into large schools in the northern Gulf and constitute the spawning stock for the species in this area.

Overstreet[1] first reported on various aspects of the biology, including reproduction, of schooling red drum based on specimens gathered from the purse-seine fishery for the species. Fitzhugh et al. (1988) added to this body of knowledge by describing ovarian development in specimens similarly taken from the purse-seine fishery. They further provided the first documentation of feral red drum as group synchronous, batch spawners (Wallace and Selman, 1981) in which clutches of newly matured ova are spawned periodically throughout the spawning season. Thus all previous estimates of red drum fecundity in the wild, based on numbers of vitellogenic oocytes present in the ovary, were rendered invalid.

The present study is a continuation and an expansion of the work begun by Fitzhugh et al. (1988) and was undertaken in conjunction with two studies of red drum age and growth (Beckman et al., 1988; Wilson et al.[2]). Our specific objectives were 1) to verify the sex ratio of the spawning population; 2) to ascertain the duration of the spawning season; 3) to determine age, length, and weight at sexual maturity; and

*Contribution LSU-CFI-93-4 of the Coastal Fisheries Institute, CCEER, Louisiana State University.

[1] Overstreet, R. M. 1983. Aspects of the biology of the red drum, *Sciaenops ocellatus*, in Mississippi. Gulf Res. Rep. (Suppl. 1), p. 45–68. Gulf Coast Res. Lab., Ocean Springs, MS.

[2] Wilson, C. A., D. L. Nieland, and A. L. Stanley. 1993. Variation of year-class structure and annual reproductive output of red drum *Sciaenops ocellatus* and black drum *Pogonias cromis* from the northern Gulf of Mexico. Final Report for 1991–1992 to U. S. Department of Commerce, Marine Fisheries Initiative (MARFIN) Program, NA90AA-H-MF724. LSU-CFI-93-3, 37 p. and 16 figs.

4) to estimate batch fecundity and spawning frequency of red drum from the neritic waters of the northern Gulf of Mexico.

Methods and materials

Red drum were sampled in the neritic waters of the northern Gulf of Mexico (Mobile Bay, Alabama westward to Galveston Bay, Texas) from March 1986 through September 1992, a period spanning seven spawning seasons. Various aspects of the reproduction of those specimens taken from March 1986 through November 1986 have been previously reported by Fitzhugh et al. (1988). The availability of red drum during this study was sporadic and generally limited by federal and state restrictions on both the commercial and recreational fisheries in the Gulf of Mexico. Although the vast majority of specimens were taken by purse seine, the strategies used to locate red drum schools for capture varied among years. Prior to the closure of the Exclusive Economic Zone to all red drum harvest in 1986, specimens came from the commercial purse-seine fishery. Red drum collected from July 1986 through 1988 were taken concurrently with a National Marine Fisheries Service tag-recapture investigation. Their methodology simulated a commercial purse-seine fishery and used spotter airplanes to locate schools at the surface. Since August 1989 most red drum were taken incidentally in the directed purse-seine harvest of blue runner, *Caranx chrysos*, detected visually at the surface.

The above samples were supplemented with specimens from sportfishing tournaments, from incidental catches of vessels targeting snappers (Lutjanidae), and from gillnet and haul-seine catches. These sources were sampled as circumstances allowed to permit tracking of ovarian development and gonosomatic indices during those months when specimens taken by purse seine were not available.

Protocols for the collection of morphometric data (fork length [FL] in mm, total weight [TW] in kg, eviscerated body weight [BW] in kg), processing of ovaries for histological examination, and enumeration of oocyte maturation stages from histological slides (Wallace and Selman, 1981; Fitzhugh et al., 1988) are given in Nieland and Wilson (1993). Histological slides were also scanned for the presence of yolk coalescence, and for postovulatory follicles and atretic follicles. Ages of individuals were estimated from sagittal otoliths as described in Beckman et al. (1988). Their methodology assumed a biologically reasonable hatching date of 1 October; however, for our purposes age estimates were calculated with 1 August as the arbitrary red drum hatching date. This modification allows all members of a cohort to be assigned the same integer year age.

Sexual maturity of females captured during the spawning season was defined as the progression of oocyte maturation to vitellogenesis (Brown-Peterson et al., 1988; Nieland and Wilson, 1993). Milt flow from the central lumen of the testes produced by gentle squeezing indicated sexual maturity in males similarly taken during the spawning season (Pearson, 1929; Brown-Peterson et al., 1988; Murphy and Taylor, 1990; Nieland and Wilson, 1993).

Only those red drum females captured by purse seine were included in calculations of spawning frequency and batch fecundity. Batch fecundity was estimated gravimetrically from fresh ovarian weights for 51 females exhibiting overt macroscopic and microscopic hydration of oocytes with the hydrated oocyte method (Hunter and Goldberg, 1980; Hunter et al., 1985). Seasonal spawning frequencies were estimated with two different methods after examination of 572 ovaries collected during the spawning seasons. The postovulatory follicle method (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985; Hunter et al., 1985; Brown-Peterson et al., 1988; Nieland and Wilson, 1993) uses the number of mature females with postovulatory follicles to determine a spawning fraction or that proportion of the female spawning population that spawned the previous day. The inverse of the spawning fraction, the spawning frequency, is the average number of days over which each reproductively active female will spawn once. The spawning frequency estimates of Fitzhugh et al. (1993), referred to as the "time-calibrated" method, are based on a time-course of final oocyte maturation for black drum, *Pogonias cromis*, and another sciaenid species, the spotted seatrout, *Cynoscion nebulosus*, (Brown-Peterson et al., 1988). This methodology calculates proportions of day-0 females (imminent spawners evidenced by oocyte yolk coalescence or hydration) and day-1 spawners (previous spawners evidenced by postovulatory follicles) in the female spawning population. The average of the proportions of day-0 and day-1 females yields a spawning fraction which is inverted to produce spawning frequency as defined above. Note that females spawning on consecutive days will be classified as both day–0 and day-1 individuals. Also those females evidencing oocyte atresia states 2 (atresia of ≥50% of vitellogenic oocytes) and 3 (atresia of 100% of vitellogenic oocytes) (Fitzhugh et al., 1993) were not included in either estimate of spawning frequency. Both conditions, usually encountered at the end of the spawning season, indicate a zero probability of future spawning and an effective exit from the spawning population (Hunter and Macewicz, 1985).

The temporal persistence of postovulatory follicles in red drum ovaries was investigated in two captive red drum that were induced to spawn by means of photoperiod manipulation and gonadotropin injection (Nieland, Wilson, and Thomas, unpubl. data). Postovulatory follicles at 16-hour postspawning showed definite signs of degeneration, yet were recognizable as such and resembled those seen in many wild caught females. However, postovulatory follicles at 24-hour postspawning were extremely degenerate and had assumed an aspect much like that of an atretic follicle. Such a condition was rare in feral specimens; thus, all identifiable red drum postovulatory follicles were assumed to be less than 24 hours old. Postovulatory follicles seen in histological material were classified as early, late, or very late based on their degree of degeneration.

Relative investment of energy to reproduction of red drum was assessed with gonosomatic indices (GSI) calculated as GSI = (gonad weight/BW) × 100 (Nieland and Wilson, 1993). Calculations of mean monthly GSI exclude immature individuals of both sexes (Wilk et al., 1990; Nieland and Wilson, 1993). Because the increase in ovary mass, which occurs concomitantly with oocyte hydration, does not reflect energy to be expended in reproduction, females with hydrating oocytes were also excluded from calculations of mean monthly GSI. The Statistical Analysis System (SAS Institute Inc., 1985) was used for analysis of variance (ANOVA), maximum-likelihood analysis (PROBIT), and linear regression (GLM). Significance level for statistical analyses was 0.05 unless indicated otherwise.

Results

A total of 3,351 red drum (1,585 males, 1,765 females) were sampled for reproductive analysis. Of these, both the intact gonad weight and BW necessary for calculation of GSI were available for 2,859 mature and 341 immature specimens. Data on ovarian histology were compiled for 1,379 mature females and 123 immature females. Age at time of capture for 3,316 red drum for which otoliths were available ranged from 1 to 36 years for males and from 1 to 39 years for females. Proportions of the younger age classes were particularly high during our 1992 sampling when 327 of 504 individuals were age 6 or less. Total weight and FL ranges among all specimens were 0.7–19.2 kg and 399–1,115 mm, respectively.

Sex ratio

Sex ratios for red drum were highly variable among source and gear categories and between mature and immature individuals within these categories (Table 1). Among all specimens and all mature specimens, females were predominant; however, immature males exceeded immature females in number by two to one. Females also outnumbered males among all mature individuals taken by sportfishing, among mature individuals caught incidentally with lutjanids, and among those captured with haul seine. Conversely, males were more common among all purse-seine specimens, all immature specimens, and immature specimens taken by all methods except for sportfishing. Sex ratios were not statistically different from 1:1 for all mature red drum captured with purse seines, for all taken incidentally with lutjanids, and for those caught in gill nets.

Seasonality

Gonosomatic indices and ovarian histological data indicated a potential 8–9 week red drum spawning season beginning in mid August and extending into October. Minimal GSI values for mature individuals were found from January to July, averaging 0.26 for males and 0.81 for females during these months (Fig. 1). Abrupt escalation of male and female GSI in August signalled potential, if not certain, spawning activity. Maximum GSI values were achieved in September followed by a return to near minimum levels

Table 1

Number of specimens sampled by sex and sex ratios for all, mature, and immature red drum collected in the northern Gulf of Mexico from March 1986 through September 1992 by source or gear of capture. No immature individuals were taken by haul seine or gill net.

Source or gear	Females	Males	Sex ratio (Female:Male)
All sources and gears	1,766	1,585	1:0.90
Mature	1,642	1,364	1:0.83
Immature	124	221	0.56:1
All purse seine	1,247	1,362	0.92:1
Mature	1,152	1,212	0.95:1*
Immature	95	150	0.63:1
All sportfishing	383	102	1:0.27
Mature	369	87	1:0.24
Immature	14	15	0.93:1*
All incidental with lutjanids	54	69	0.78:1*
Mature	39	13	1:0.33
Immature	15	56	0.27:1
Haul seine	43	11	1:0.26
Gill net	39	41	0.95:1*

* Not significantly different from 1:1 (chi-square test, df=1, $P<0.05$).

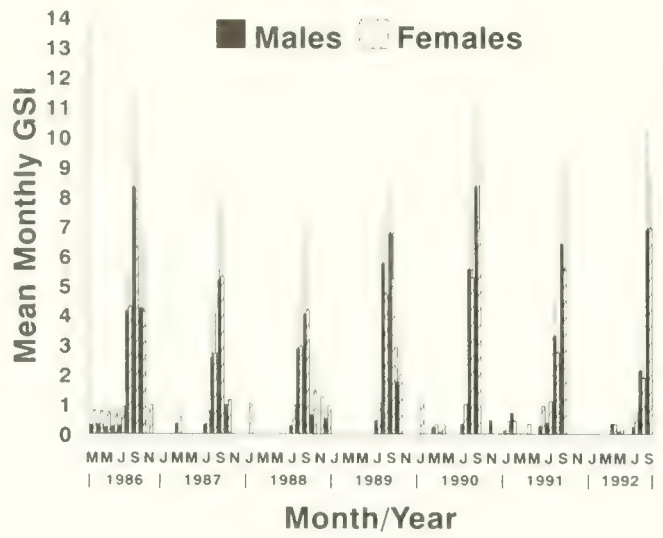

Figure 1

Mean monthly gonosomatic indices for mature male (n=1,306) and female (n=1,553) red drum from the northern Gulf of Mexico. Sample sizes for months during which red drum were available varied from 1 to 110 for males and from 1 to 183 for females. Absence of vertical bar for either sex indicates that no specimens were sampled during the month and year indicated below. Narrow vertical bars at tops of GSI bars indicate +1 standard deviation (SD) from mean value (plotted only for those months when SD>0.5).

in October. Our data, collected over more than six years, demonstrated a single annual GSI maximum (ranging from 4 to 8) in each sex.

Red drum ovarian tissues undergo an annual cycle of oocyte maturation and recrudescence coincident with the female GSI cycle. Over the entire study duration, oogonia and primary growth oocytes were present in varying numbers in all ovary samples but were virtually ubiquitous from January through June (Fig. 2). Recrudescence and maturation of primary growth oocytes to the cortical alveoli and vitellogenic stages, indicative of preparation for spawning, was seen in July. Maximum numbers of maturing vitellogenic and mature hydrated oocytes were found during August and September. Declines in numbers of cortical alveolar and vitellogenic oocytes and concomitant increases in numbers of primary growth oocytes occurred in October suggesting the cessation of spawning activity at this time. Although we have few data from November and December, primary growth oocytes are assumed to constitute nearly 100% of the oocyte population during these months.

Among all spawning seasons, the onset of spawning activity, evidenced by the first observation of yolk coalescence (late vitellogenesis) or postovulatory follicles in ovarian histological samples, ranged from 14 August to 18 August. Atretic states 2 and 3, indicative of cessation of spawning, became increasingly common from late September through early October. When we were able to extend our sampling in 1987 and 1988, 100% atresia of vitellogenic oocytes was realized by the end of October indicating completion of spawning at this time.

Age, length, and weight at maturity

The onset of sexual maturity in both male and female red drum in the northern Gulf of Mexico is variable with respect to age. Estimates of percent maturity at age are comparable and increase at much the same rate for both sexes, the only major discrepancies occurring at age 2 and age 5 (Table 2). Greater than 50% maturity is achieved in both sexes at age 4. All males and all females are mature at age 5 and age 6, respectively.

Sexual maturity in red drum is similarly unrelated to size of the individual (Table 2). Fork length and TW minima among mature female red drum were 598 mm (age 4, 4.18 kg) and 3.43 kg (age 3, 675 mm). Maximum-likelihood analysis (PROBIT analysis, Murphy and Taylor, 1989) of 10 mm increments and of 0.10 kg increments indicated 50% maturity is achieved at 690–700 mm and 4.00–4.10 kg. All females greater than 810 mm and 6.10 kg were mature.

Male red drum from the northern Gulf of Mexico mature at somewhat lesser length and weight than do females; however, sex-specific percent maturities at size become roughly equivalent at 750–700 mm and 5.00–5.49 kg (Table 2). Fork length and TW minima for mature males were 593 mm (age 5, 2.56 kg) and 2.35 kg (age 2, 615 mm). Fifty percent maturity (maximum-likelihood analysis as above) occurred at 660–670 mm and 3.40–3.50 kg and all males greater than 810 mm and 5.40 kg had matured.

We observed no instances of decreased or arrested gonadal development among older individuals. Red drum of both sexes appear to be fully capable of reproductive activity from the onset of maturity until death.

Batch fecundity

Fitzhugh et al. (1988) reported significant ovarian location effects in their estimates of red drum batch fecundity. To test the precision of our estimates within individuals, replicate samples (30–60 mg) of ovarian tissue from each of six ovarian regions (anterior, medial, and posterior of both right and left lobes) were removed from six hydrated females captured

26 September 1988. Numbers of hydrated oocytes per gram of ovarian tissue were calculated for each sample (n=72). Nested ANOVA showed significant variation only among individuals; no location effects were demonstrated (Table 3). All individual batch fecundities herein are means of estimates made from three different randomly selected regions as defined above.

Batch fecundity estimates were generated for a combined sample of 51 red drum captured by purse seine during the 1986 (previously reported by Fitzhugh et al. (1988)), 1987, 1988, 1989, and 1991 spawning seasons. All displayed overt macroscopic and microscopic manifestations of oocyte hydration throughout the length and diameter of the ovarian lobes and were captured during the late afternoon or early evening hours (1600–1900 h). No sufficiently hydrated females were encountered in 1990 and 1992.

Age, FL, batch fecundity ranges, and numbers of hydrated specimens examined by year of capture are given in Table 4. Regression analyses of batch fecundity against FL (r^2=0.58), gonad-free body weight (r^2=0.46), age in year (r^2=0.43), and BW (r^2=0.43) are of reasonable predictive value (Fig. 3). Significant positive relations (P>0.0001) were indicated between batch fecundity and nontransformed values of the four independent variables. The relatively low r^2 values for the regressions appear to result from individual varia-

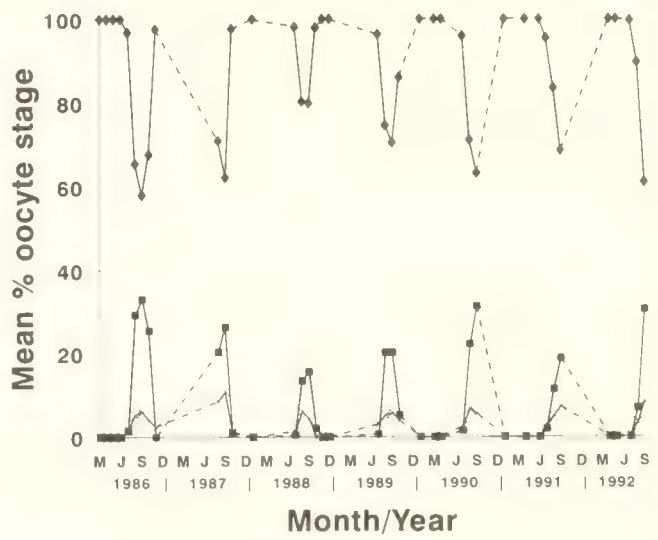

Figure 2

Monthly mean percent occurrence of primary growth (diamonds), cortical alveoli (crosses), and vitellogenic (squares) oocytes in ovaries of red drum from the northern Gulf of Mexico. Total sample size is 1,379; for months during which female red drum were available, sample size ranged from 1 to 160. Dashed lines span months during which specimens were unavailable. Ranges of standard deviations (SD) during August–October were 3.4–18.3 for primary growth oocytes, 0.0–3.4 for cortical alveoli oocytes, and 2.2–13.1 for vitellogenic oocytes.

Table 2

Percent maturity and numbers sampled (in parentheses) of female and male red drum at age, fork length, and total weight. Specimens included are those taken by all gears during August through October of 1986–1991 and August and September 1992. Total sample sizes are 1,262 females and 1,137 males.

Class	Female	Male	Class	Female	Male
Age (years)			Fork length (mm)		
1	0 (0)	0 (0)	750–799	95 (129)	97 (178)
2	0 (8)	13 (24)	800–849	99 (216)	99 (280)
3	28 (81)	30 (148)	≥850	100 (764)	100 (391)
4	71 (75)	73 (88)			
5	88 (68)	100 (77)	Total weight (kg)		
≥6	100 (1,011)	100 (787)	<3.00	0 (45)	13 (96)
			3.00–3.49	8 (24)	35 (54)
			3.50–3.99	33 (18)	60 (40)
Fork length (mm)			4.00–4.49	75 (28)	84 (31)
<550	0 (7)	0 (15)	4.50–4.99	83 (23)	90 (52)
550–599	8 (13)	8 (25)	5.00–5.49	94 (33)	97 (39)
600–649	0 (26)	22 (68)	5.50–5.99	95 (60)	100 (55)
650–699	24 (42)	48 (82)	6.00–6.49	98 (59)	100 (79)
700–749	82 (65)	91 (98)	≥6.50	100 (963)	100 (678)

Table 3

Nested analysis of variance on numbers of hydrated oocytes per gram ovary weight among ovarian regions (six total-three per lobe), between ovarian lobes (right and left), and among six female red drum captured 26 September 1988 from the northern Gulf of Mexico. MS=mean square.

Source of Variation	df	MS	*F*-value	*P*>*F*-value
Individuals	5	42,580,790	69.86	0.0001
Lobes	6	242,773	0.33	0.9155
Ovarian regions	24	2,290,678	0.78	0.7318
Error	36	4,266,679		
Total	72	49,380,920		

Table 4

Age, fork length (FL), and batch fecundity (BF) ranges for red drum *Sciaenops ocellatus* from the northern Gulf of Mexico by year of capture. *n*=number of specimens.

Year	*n*	Age range (yr)	FL range (mm)	BF range (ova × 10^6)
1986	8	6–21	800–964	0.75–2.54
1987	2	20–33	933–1005	1.65–1.67
1988	6	9–30	820–950	1.87–3.22
1989	23	3–24	697–999	0.16–3.27
1990	0	—	—	
1991	12	5–25	760–924	0.57–3.13
1992	0	—	—	—
Total	51	3–33	697–1005	0.16–3.27

Table 5

Comparison of red drum seasonal spawning frequencies (SF, expressed as average days between successive spawnings) estimated with the postovulatory follicle (POF) method of Hunter and Macewicz (1985) and the time-calibrated (TC) method of Fitzhugh et al. (1993). Day-0 females are those evidencing yolk coalescence or hydration of oocytes; day-1 females are those with postovulatory follicles from previous day's spawning. All specimens collected by purse seine from 13 August through 8 October.

		POF method		TC method		
Year	Mature females	Females with POF	SF	Day-0 females	Day-1 females	SF
1986	39	14	2.8	24	14	2.1
1987	79	17	4.6	36	17	3.0
1988	155	14	11.1	65	14	3.9
1989	91	17	5.4	36	17	3.4
1990	57	1	57.0	28	1	3.9
1991	80	1	80.0	51	1	3.1
1992	71	1	71.0	2	1	47.3
Total	572	65	8.8	242	65	3.7

tion within classes. Exclusion from the regression analyses of those specimens captured during October, based on the possibility of declining output toward the end of the spawning season as suggested by Fitzhugh et al. (1988), produced r^2 values ranging from 0.23 to 0.39.

Spawning frequency

Red drum spawning frequencies estimated with the postovulatory follicle method were highly variable among years (Table 5) ranging from one spawning event every 2.8 days in 1986 to one spawn every 80.0 days in 1991. A total of 65 of 572 sexually mature females captured during the 1986–1992 spawning seasons evidenced postovulatory follicles for a seven season average spawning frequency of 8.8 days. Spawning frequencies calculated with the time-calibrated method (Table 5) showed less variation and gave more plausible estimates. Except for the 1992 spawning season, when sampling was limited to three dates during the spawning season (28 August, 3, 12 September), spawning frequencies of one spawn every 2–4 days were predicted.

Discussion

Aspects of red drum reproductive biology in the Gulf of Mexico have been variously inferred from visual observation of gonadal development, from larval and juvenile abundances and lengths, and from histological documentation of ovarian development. Given both the disparities and subjectivity inherent among, and even within, these methodologies and the expanse of the Gulf of Mexico, it is not surprising that published accounts of red drum reproduction vary widely and, perhaps, geographically. We agree with West (1990) that histological methods produce the most accurate and most reliable results in assessing ovarian development and predicting reproductive variables. We also stress that our findings should not be broadly applied to red drum populations throughout the Gulf of Mexico.

The sex ratio of the 2,364 mature individuals taken by purse seine is undoubtedly most reflective of the offshore spawning stock of red drum in the northern Gulf of Mexico. Given that most of our specimens taken by purse seine were captured either just prior to or during the spawning season and considering the substantial sample size, our data establish a 1:1 sex ratio in schools of prespawning and spawning red drum. This supports

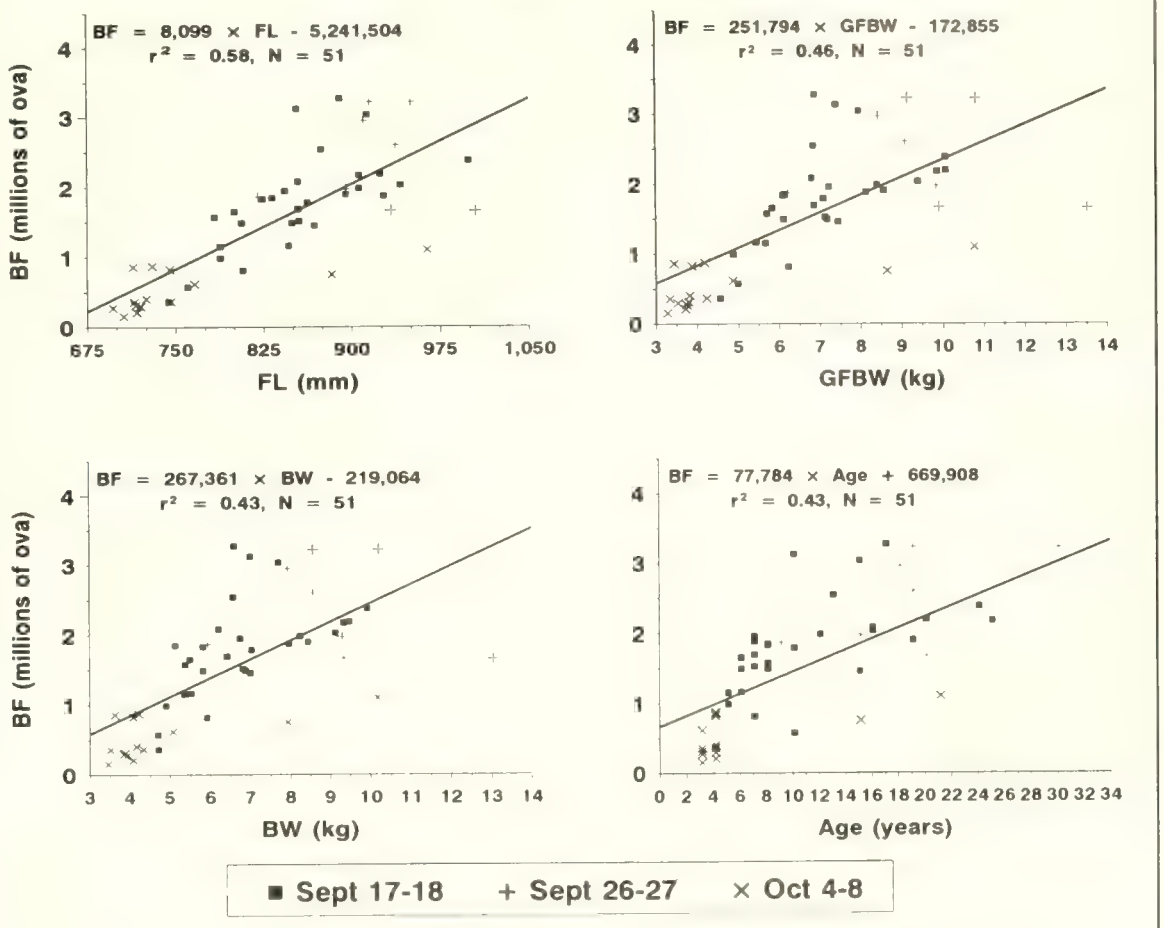

Figure 3

Regressions of eviscerated body weight (BW), fork length (FL), gonad-free body weight (GFBW), and age versus estimated batch fecundity for red drum from the northern Gulf of Mexico. Squares denote specimens captured on 17 September 1986 and 18 September 1991, pluses on 26 September 1988 and 27 September 1987, and crosses on 4 October 1989 and 8 October 1986. *n*=total sample size.

and further validates the use of a 1:1 ratio by Comyns et al. (1991) in their estimation of red drum spawner biomass in the north-central Gulf of Mexico.

For immature red drum, males significantly outnumbered females across all source and gear categories except among the few specimens randomly encountered at sportfishing tournaments. This numerical dominance of immature male red drum in offshore waters may indicate a predisposition for emigration from estuarine habitats at younger age than females which is reflected in the somewhat lesser age and size at maturity seen in males.

Previous accounts of red drum seasonality in the northern Gulf of Mexico have relied on inferences drawn from postspawning capture of larvae and juveniles and, to a lesser extent, from visual assessment of ovaries and testes. The red drum spawning season has been variously estimated with these methodologies as September to December (Boothby and Avault, 1971), August to November (Sabins, 1973), and from early September to early October (Comyns et al., 1991). However, our delineation of a mid-August to early October red drum spawning season is in accord with other studies that used histological techniques. Within our study area, analyses of red drum oocyte maturation by Overstreet[1] in Mississippi and by Fitzhugh et al. (1988) in Louisiana both demonstrated that red drum spawning is initiated in August and continues into October. Murphy and Taylor (1990) found spawning red drum from August to mid-November 1981 and from August to mid-October 1982 in the Tampa Bay, Florida area. The concordance among these estimates, drawn objectively and directly from histological data, dem-

onstrates the effectiveness of this technique in assessing onset and duration of spawning seasons.

Determining the combination of environmental factors which are the impetus for an August-October red drum spawning season is beyond the scope of this study. However, temperature data gathered at a weather buoy located approximately 28 km south of Biloxi, MS (lat. 30.1°N, long. 88.8°W) indicate that seasonal mean sea surface temperatures ranged from 27.3° to 28.8°C and that daily mean sea surface temperatures varied from 23° to 31°C during periods of active spawning (National Climatic Data Center, Asheville, North Carolina). Similar temperatures have proven to be optimal in the spawning, hatching, and rearing of red drum in the laboratory (Arnold et al., 1977; Roberts et al., 1978; Holt et al., 1981; Arnold, 1988; Henderson-Arzapalo, 1992).

Estimates of age and size at maturity for red drum in the Gulf of Mexico, based largely on visual assessment of gonadal development, show extensive variation. In his study of red drum in Texas waters, Pearson (1929) perhaps originated the long held and widely applied belief that few red drum of either sex mature either before age 5 or before attaining 10 lb (4.5 kg) and 700 mm. Among red drum populations in Texas waters, maturity has been reported at 425 mm (Gunter, 1950), 625 mm (Miles[3]), age 4 and 29.5 inches (750 mm) (Miles[4]), and age 3 to 5 (Holt et al., 1981). For red drum off Mississippi, Overstreet[1] provided only a tabular compilation of the relation between standard length (SL) and gonad maturity stages. These data were interpreted by Murphy and Taylor (1990) to show 50% maturity in both sexes at about 700 mm SL. Murphy and Taylor also presented maturity schedules, which were based on histology of ovaries and testes and gross appearance of each, for red drum in Florida waters. They found fifty-percent maturity of males at 529 mm FL and all males mature at age 3; among females 50% and 100% maturity occurred at 825 mm FL and 6 years, respectively.

Given the maturity data cited above and that of the present study, one might infer the existence of geographical variation in maturity schedules among red drum populations in the Gulf of Mexico. We decline to discount this possibility. However, we suggest that differences in methods of maturity assessment and disparate definitions of maturity, especially in females, confound comparisons. West (1990) reviewed methods of assessing ovarian development in fishes and concluded that histology, though less efficient in both cost and time, is less subjective than, and preferable to, other methodologies.

For the purposes of the present study, we defined maturity in male red drum as the flow of milt from the central lumen of the testis during the August–October spawning season. The use of this subjective definition may account for some of the discrepancy in male maturity schedules between our study and that of Murphy and Taylor (1990).

However, for assessment of the maturity schedule of female red drum in the northern Gulf we employed a histologically objective benchmark definition: the presence of vitellogenic oocytes in the ovaries of individuals captured during the spawning season. Murphy and Taylor (1990) considered as mature only those females of class 4 (late vitellogenesis) or greater among their eight female reproductive classes in estimating an 825 mm FL at 50% maturity. This necessitated the categorization of out-of-season females (their class 2) and of in-season females evidencing early vitellogenesis (their class 3) as immature. The former would not have been included in our analysis of female maturity; the latter would have been classified as mature under our definition which precludes judgments between early and late vitellogenesis. A cautious re-interpretation of the tabular data in Overstreet[1] would yield greater than 50% maturity of females at 550–699 mm SL rather than the >700 mm SL as stated by Murphy and Taylor (1990). Applying our definition of maturity to Murphy and Taylor's data would perhaps produce a length at 50% maturity more in line with our estimate of 690–700 mm FL.

Group-synchronous maturation of oocytes (Wallace and Selman, 1981) and multiple, or batch, spawning has been demonstrated in several species of sciaenid fishes, including red drum (Fitzhugh et al., 1988). Among these are queenfish, *Seriphus politus* (DeMartini and Fountain, 1981); black croaker, *Cheilotrema saturnum* (Goldberg, 1981); white croaker, *Genyonemus lineatus* (Love et al., 1984); spotted seatrout (Brown-Peterson et al., 1988); and black drum (Fitzhugh et al., 1993; Nieland and Wilson, 1993). For these and other such species, the standing crop of oocytes of some arbitrary size or of vitellogenic oocytes gives little indication of the individual's seasonal fecundity. Rather fecundity is indeterminate and is the result of clutches of oocytes matured and spawned periodically over the length of the spawning season. Thus any estimate of seasonal fecundity must consider the length of the spawning season, the number of ova released in each spawning event (batch fecundity), and the periodicity of these spawning events (spawning frequency).

[3] Miles, D. W. 1950. The life histories of the spotted sea trout, *Cynoscion nebulosus*, and the redfish, *Sciaenops ocellatus*. Annu. Rep. (1949–1950), Tex. Game and Fish Comm. Mar. Lab., p 66–103. Tex. Parks and Wildl. Dept., Austin.

[4] Miles, D. W. 1951. The life histories of the sea-trout, *Cynoscion nebulosus*, and the redfish, *Sciaenops ocellatus*: sexual development. Annu. Rep. (1950–1951), Tex. Game and Fish Comm. Mar. Lab., 11 p., 2 figs., and 3 tables. Tex. Parks and Wildl. Dept., Austin.

Prior to the confirmation of batch spawning in feral red drum by Fitzhugh et al. (1988), fecundity of wild caught specimens had been variously estimated as 0.5–3.5 million ova per season (Pearson, 1929; Holt et al., 1981; Miles[5]). Much greater potential fecundities (up to 94.5 million), based on volumetric and gravimetric estimates of oocytes available for spawning, were presented by Overstreet[1]. This potential for an immense seasonal reproductive output in wild red drum has been demonstrated in the laboratory where specimens have been manipulated to produce repeatedly a few hundred thousand to millions of ova per spawning event (Arnold et al., 1977; Roberts et al., 1978; Anonymous, 1979; Arnold, 1988). Other than the batch fecundity estimates for feral red drum presented by Fitzhugh et al. (1988) and those herein, only one other estimate has appeared in the literature. Comyns et al. (1991), from our data for September of 1986, 1987, and 1988, used a mean batch fecundity of 2.128 million ova in their computations of red drum spawner biomass in the north-central Gulf of Mexico.

Our seasonal estimates of spawning frequency are the first to be presented for red drum in the wild. Those seasonal frequencies (3–5 d) calculated for 1986, 1987, and 1989 with the postovulatory method and those (2–4 d) calculated for 1986–1991 with the time-calibrated method are believed to be most representative of the spawning population as similar spawning frequencies have been observed in the laboratory (Arnold et al., 1977; Arnold, 1988). However, spawning frequency is likely not constant over the course of the spawning season. Within-season spawning peaks coinciding with the new and full moon have been postulated by Peters and McMichael (1987) and Comyns et al. (1991) based on larval abundances. The irregularity of our sampling precluded our investigation of this phenomenon.

Given an 8–9 week spawning season, a mean batch fecundity of 1.54 million ova, and a spawning frequency of 2–4 days, an average red drum female could be expected to spawn some 20–40 million ova per season. Among sciaenid species, this estimate of annual fecundity is exceeded only by that of the black drum, a species of similar size which has an annual fecundity of 35–45 million ova (Nieland and Wilson, 1993). Females of both species are potentially long-lived (30–35 yr) and, thus, might produce up to a billion of ova during their lifetimes.

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Literature cited

Anonymous.
1979. Redfish spawn produces 11.4 million fry. Texas Parks Wildl. 37(7):15.

Arnold, C. R.
1988. Controlled year-round spawning of red drum *Sciaenops ocellatus* in captivity. Contrib. Mar. Sci., Suppl. to vol. 30:65–70.

Arnold, C. R., W. H. Bailey, T. D. Williams, A. Johnson, and J. L. Lasswell.
1977. Laboratory spawning and larval rearing of red drum and southern flounder. Proc. Annu. Conf. S.E. Fish and Wildlife Agencies 31:437–440.

Beckman, D. W., C. A. Wilson, and A. L. Stanley.
1988. Age and growth of red drum, *Sciaenops ocellatus*, from offshore waters of the northern Gulf of Mexico. Fish. Bull. 87:17–28.

Boothby, R. N., and J. W. Avault Jr.
1971. Food habits, length-weight relationship, and condition factor of the red drum (*Sciaenops ocellatus*) in southeastern Louisiana. Trans. Am. Fish. Soc. 100:290–295.

Brown-Peterson, N., P. Thomas, and C. R. Arnold.
1988. Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in South Texas. Fish. Bull. 86:373–388.

Comyns, B. H., J. Lyczkowski-Schultz, D. L. Nieland, and C. A. Wilson.
1991. Reproduction of red drum, *Sciaenops ocellatus*, in the northcentral Gulf of Mexico: seasonality and spawner biomass. *In* R. D. Hoyt (ed.),

Larval fish recruitment and research in the Americas, p. 17–26. Dep. Commer., NOAA Tech. Rep. NMFS 95.

DeMartini, E. E., and R. K. Fountain.
1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull. 79:547–560.

Fitzhugh, G. R., T. G. Snider III, and B. A. Thompson.
1988. Measurement of ovarian development in red drum (*Sciaenops ocellatus*) from offshore stocks. Contrib. Mar. Sci., Suppl. to vol. 30:79–83.

Fitzhugh, G. R., B. A. Thompson, and T. G. Snider III.
1993. Ovarian development, fecundity, and spawning frequency of black drum *Pogonias cromis* in Louisiana. Fish. Bull. 91:244–253.

Goldberg, S. R.
1981. Seasonal spawning cycle of the black croaker, *Cheilotrema saturnum* (Sciaenidae). Fish. Bull. 79:561–562.

Gunter, G.
1950. Correlation between temperature of water and size of marine fishes on the Atlantic and Gulf coasts of the United States. Copeia 1950:298–304.

Henderson-Arzapalo, A.
1992. Red drum aquaculture. Rev. Aquat. Sci. 6:479–491.

Holt, J., A. G. Johnson, C. R. Arnold, W. A. Fable Jr., and T. D. Williams.
1981. Description of eggs and larvae of laboratory reared red drum, *Sciaenops ocellata*. Copeia 1981:751–756.

Hunter, J. R., and S. R. Goldberg.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull. 77:641–652.

Hunter, J. R., and B. J. Macewicz.
1985. Measurement of spawning frequency in multiple spawning fishes. *In* R. L. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, p. 79–94. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong.
1985. Batch fecundity in multiple spawning fishes. *In* R. L. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, p. 67–77. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Love, M. S., G. E. McGowen, W. Westphal, R. J. Lavenberg, and L. Martin.
1984. Aspects of the life history and fishery of the white croaker, *Genyonemus lineatus* (Sciaenidae), off California. Fish. Bull. 82:179–198.

Murphy, M. D., and R. G. Taylor.
1989. Reproduction and growth of black drum, *Pogonias cromis*, in northeast Florida. Northeast Gulf Sci. 10:127–137.
1990. Reproduction, growth, and mortality of red drum, *Sciaenops ocellatus*, in Florida waters. Fish. Bull. 88:531–542.

Nieland, D. L., and C. A. Wilson.
1993. Reproductive biology and annual variation of reproductive variables of black drum in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 122:318–327.

Pearson, J. C.
1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. U.S. Bur. Fish. Bull. 44:129–214.

Peters, K. M., and R. H. McMichael Jr.
1987. Early life history of *Sciaenops ocellatus* (Pisces: Sciaenidae) in Tampa Bay, Florida. Estuaries 10:92–107.

Roberts, D. E., Jr., B. V. Harpster, and G. E. Henderson.
1978. Conditioning and induced spawning of the red drum (*Sciaenops ocellata*) under varied conditions of photoperiod and temperature. Proc. World Maricult. Soc. 9:311–332.

Sabins, D. S.
1973. Diel studies of larval and juvenile fishes of the Caminada Pass area, Louisiana. M.S. thesis, Louisiana State Univ., Baton Rouge, 163 p.

SAS Institute.
1985. SAS user's guide: statistics, version 5 ed. SAS Institute Inc., Cary, NC, 956 p.

Wallace, R. A., and K. Selman.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

West, G.
1990. Methods of assessing ovarian development in fishes: a review. Aust. J. Mar. Freshwater Res. 41:199–222.

Wilk, S. J., W. W. Morse, and L. L. Stehlik.
1990. Annual cycles of gonad-somatic indices as indicators of spawning activity for selected species of finfish collected from the New York Bight. Fish. Bull. 88:775–786.

Biology and population characteristics of *Squalus mitsukurii* from a seamount in the central North Pacific Ocean

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Abstract.—Little information exists on the biology of the demersal shark, *Squalus mitsukurii*. Recently, large numbers of this species were taken incidentally during research surveys conducted at Southeast Hancock Seamount in the central North Pacific Ocean. The information collected during 1985 to 1988 from these surveys is used to describe the life history, depth distribution, and biology of *S. mitsukurii*.

Bathymetric distributional patterns of female and male *S. mitsukurii* differed slightly, although bottom longline catches revealed a depth distribution extending from the summit (260 m) to 740 m for both sexes. Males generally were found deeper than females. In addition, the size of males generally increased with depth whereas no apparent trend was observed for females.

Reproductive parameters for both sexes are presented. Males tended to reach maturity at smaller sizes than did females. Gravid females had broods of up to six uterine embryos. Length of young close to parturition was 21–26 cm.

Tentative estimates of age and growth were made from dorsal spine increment counts. Maximum ages were 27 years for females and 18 years for males. Females exhibited more rapid growth than males after about age 9.

The diet of *S. mitsukurii* included both benthic and mesopelagic prey. Fishes, cephalopods, and crustaceans were the major components of the diet.

Comparison of the biological characteristics suggest that this species is probably typical of other slow-growing, low fecund members of the genus *Squalus*. The 50% decline in catch rates observed during this study suggests that the number of *S. mitsukurii* on the seamount declined dramatically, possibly as a result of overfishing.

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The discovery of large stocks of the pelagic armorhead, *Pseudopentaceros wheeleri*, on seamounts of the southern Emperor-northern Hawaiian Ridge by Soviet fishermen in 1967 signaled the inception of a large, intense foreign trawl fishery for this species during the early 1970's (Uchida and Tagami, 1984). During 1967–75, for example, nearly one million metric tons of pelagic armorhead were taken from this area by Japanese and Russian trawlers (Boehlert and Genin, 1987). By the mid-1970's, catch rates of pelagic armorhead had declined dramatically, and commercial fishing for the species effectively ceased by 1984. The National Marine Fisheries Service (NMFS) initiated research stock-surveys of the area in 1985, and in August 1986 a six-year fishing moratorium was enacted (NMFS, 1986).

Results from the NMFS surveys provided information to describe the population dynamics of *P. wheeleri* (Somerton and Kikkawa, 1992). However, the population biology of several other fish species which were caught incidentally in large numbers during the NMFS surveys was largely unknown. One example was the demersal shark, *Squalus mitsukurii*, which represented the largest bycatch in the NMFS survey data (Somerton[1]).

Little is known about the life history and population dynamics of *S. mitsukurii* (Compagno, 1984) in contrast to the more cosmopolitan congener *S. acanthias* which has been extensively studied (Compagno, 1984; Ketchen, 1986). *Squalus mitsukurii* is broadly distributed in the Pacific and Indian Oceans (Compagno, 1984; Parin, 1987). Specimens resembling *S. mitsukurii* have also been taken in the Atlantic although their taxonomic status is unclear (Compagno, 1984). *Squalus mitsukurii* is known to inhabit the waters around various islands and seamounts in addition to coastal waters (Parin, 1987; Taniuchi et al., 1993). Litvinov (1990) reported on several aspects of the biology of *S. mitsukurii* from 117 specimens taken from the Sala-y-Gomez Seamounts in the Southeast Pacific. Off southeast Africa, Bass et al. (1976) presented limited information on the life history of *S. mitsukurii*, which had earlier been identified as *S. blainvillei* (Bass et

[1] Somerton, D. National Marine Fisheries Service, Seattle, WA 98115. Personal commun., 1992.

al., 1986). Whether populations of *S. mitsukurii* from different geographic areas exhibit the high variability in life history characteristics reported for *S. acanthias* (Ketchen, 1972, 1986; Compagno, 1984; Nammack et al., 1985) is unclear. The aim of the present study was to provide information on the biology and population characteristics of *S. mitsukurii* using a larger number of specimens than had previously been available, and thus elucidate its role as a member of the unique fauna associated with seamounts in the central North Pacific Ocean.

Methods

Squalus mitsukurii specimens were collected aboard the NOAA ship *Townsend Cromwell* during nine cruises to Southeast (SE) Hancock Seamount from January 1985 to November 1988 (Table 1). The seamount is located on the northern Hawaiian Ridge in the central North Pacific Ocean at lat. 29°48'N and long. 179°04'E (Fig. 1). It has a circular, flat-topped summit with an area of about 4.5 km^2 at a depth of 260 m. The seamount flanks have an average slope of 0.22 and reach bottom depths of 5,200 m about 22 km away from the summit (Brainard, 1986). Water temperatures generally are 13°–15°C at 260 m depth (i.e. summit) and decrease to 4°–6°C by 750 m (Brainard, 1986).

Most *S. mitsukurii* were collected with bottom longline gear (Somerton and Kikkawa, 1992; Shiota[2]), although a few specimens were also taken by bottom trawl, handline, vertical longline, and one set with a 25-mm square mesh bottom gill net (Table 1). Only data from hook-caught specimens were used (except for the food habits portion of the study) to avoid any bias due to differences in gear selectivity. Sets were conducted primarily during daylight hours, between the summit depth and 744 m.

All specimens of *S. mitsukurii* from a set, or a random subsample from large catches, were processed. Fish were sexed and weighed to the nearest 10 g.

[2] Shiota, P. M. 1987. A comparison of bottom longline and deep-sea handline for sampling bottom fishes in the Hawaiian archipelago. Honolulu Lab., Southwest Fish. Cent. Natl. Mar. Fish. Cent. Admin. Rep. H-87-5, 18 p.

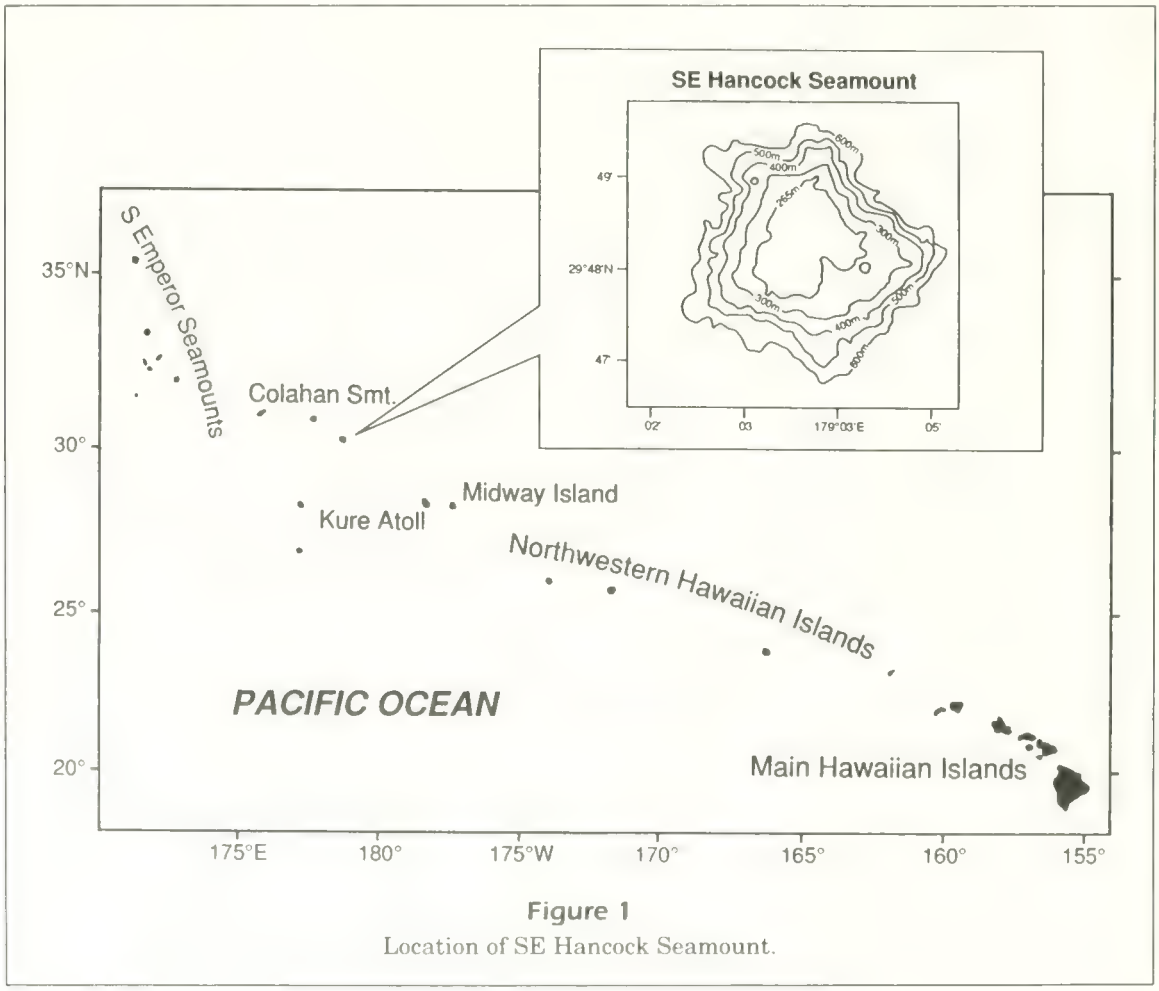

Figure 1
Location of SE Hancock Seamount.

Table 1

Catch by gear type, effort by bottom longline gear, and catch per unit of effort (CPUE; bottom longline catch per total number of hooks minus those with pelagic armorhead, *Pseudopentaceros wheeleri*) for *Squalus mitsukurii* from research operations at the SE Hancock Seamount during 1985–88. A dash indicates a particular gear type was not used on a cruise.

	Catch (no.)					Effort (no. hooks)		
Date	Bottom trawl	Handline	Vertical longline	Gill net	Bottom longline	Total	Total minus armorhead	CPUE
Winter 1985 (1/30–2/25)	1	66	—	—	335	2,001	1,607	0.208
Summer 1985 (6/19–7/16)	0	10	56	—	521	2,659	1,995	0.261
Summer 1986 (8/11–9/9)	8	—	—	42	506	6,568	4,208	0.120
Fall 1986 (10/31–11/12)	0	—	—	—	339	2,783	1,944	0.174
Spring 1987 (4/11–28)	20	5	—	—	218	3,218	2,243	0.097
Summer 1987 (8/8–25)	19	—	—	—	228	4,182	3,646	0.063
Winter 1988 (1/12–30)	4	—	—	—	253	3,546	2,842	0.089
Summer 1988 (7/13–8/21)	—	—	—	—	182	5,500	4,171	0.044
Fall 1988 (10/26–11/8)	—	—	—	—	219	4,067	2,921	0.075

Total length (TL) was determined to the nearest 1 mm by placing the shark on its side and measuring from the anterior tip of the snout to the posterior edge of the upper lobe of the caudal fin in the "natural" upright position. For some specimens, body length (STL) was measured from the anterior tip of the snout to the posterior edge of the upper lobe of the caudal fin after the lobe was depressed to a position in line with the body axis; fork length (FL) was also measured from the snout to the fork or middle of the caudal fin. Simple linear regression relationships among the three length measurements were determined to facilitate comparisons with other published studies. The relationships are $TL = 1.08 \times LF + 1.67$ ($r^2 = 0.99$, $n = 342$); $TL = 0.95 \times \mathrm{STL} + 0.24$ ($r^2 = 0.99$, $n = 212$); $STL = 1.01 \times FL + 6.31$ ($r^2 = 0.91$, $n = 463$).

A nonlinear estimation procedure (Wilkinson, 1988) was used to fit individual length and weight (WT; in grams) data to the relationship, $WT = a \times TL^b$. Weight-length relationships between sexes were evaluated with analysis of covariance (ANCOVA) on the log-transformed data.

Catch per unit of effort (CPUE) for *S. mitsukurii* was determined by using only specimens taken by bottom longline for several reasons. The bottom trawl, handline, and gillnet gear did not have fishing effort comparable with the bottom longline, and the former data were too limited to construct individual time series for each gear. Furthermore, the vertical longline gear was used to define the vertical distribution of pelagic armorhead above the summit; therefore only a few hooks of uncertain number were on the summit and available to *S. mitsukurii*. Finally, specimens from gear other than bottom longline accounted for only 8% of the total numbers caught. Therefore, it was unlikely that the exclusion of these data from the CPUE calculations would significantly bias our results. Fishing effort on *S. mitsukurii* was expressed in number of hooks set, minus hooks that caught pelagic armorhead. Pelagic armorhead respond more quickly to the bottom longline than do *S. mitsukurii* (Somerton[3]). Thus, excluding those hooks occupied by pelagic armorhead, although not removing all bias from the species-gear interaction, likely improved estimates of fishing effort on *S. mitsukurii* over the unadjusted value.

An estimate of the initial exploitable biomass of *S. mitsukurii* was made with the Leslie model (Ricker, 1975) in which a linear function was fitted to CPUE and cumulative catch data from all cruises. The function has a slope equal to catchability (q) and intercept equal to the product of q and the initial exploitable biomass. The model assumes that changes in CPUE over time are due to fishing and that other sources of losses and additions to the population are relatively minor or in balance (e.g. natural mortality and recruitment). The 95% confidence limit on the abundance estimate was calculated by using the method of Polovina (1986).

First and second dorsal spines were collected during the summer of 1986 for ageing *S. mitsukurii* with procedures outlined by McFarlane and Beamish (1987). All age results were based on the second

[3] Somerton, D. National Marine Fisheries Service, Seattle, WA 98115. Personal commun., 1992.

dorsal spine which was considered most suitable for ageing (also see Litvinov, 1990). All ridges on the surface of the mantle covering the spine were counted by a single reader with a low-power dissecting scope and methods described by Ketchen (1975) and Beamish and McFarlane (1985). No ridges were grouped and counted as a single "annulus" as was done in several earlier studies (e.g. Holden and Meadows, 1962). Loss of increments due to abrasion of the tip of the spine has been reported for other species of *Squalus* (e.g. Ketchen, 1975), but this did not occur in the present study. For example, when a worn spine was observed, the worn area was confined to the region of the spine tip having a diameter of <3 mm. However, unworn spines having spine base diameters of ≤3 mm had not yet formed any increments (the spine base diameter of a late-term uterine embryo was 2.0 mm).

Validation of the annual nature of spine increment formation (following the methods described by McFarlane and Beamish [1986, 1987]) was not possible. Therefore increment counts from spines reported here must be considered as tentative estimates of age. Nonetheless, validation studies conducted on *S. acanthias* have verified that spine increments do represent annual marks (Beamish and McFarlane, 1985; Tucker, 1985).

Individual length-at-age data for each sex were fitted with a nonlinear estimation procedure (Wilkinson, 1988) to the von Bertalanffy growth model (Ricker, 1975):

$$L_t = L_\infty \left(1 - e^{(-k(t-t_0))}\right),$$

where L_t is length at age, L_∞ is asymptotic length, k is the growth coefficient, and t_0 is the theoretical age when $L_t = 0$.

Reproductive data were first collected from shark specimens during the summer of 1986. For females, counts were made of mature ovarian eggs (greater than about 2.5 cm diameter), candled embryos (i.e. gelatinous uterine capsules containing embryos in early stages of development), and embryos free in the uteri. Females possessing any or all of these reproductive products were considered sexually mature. Sex and TL of uterine embryos were also recorded. Ketchen (1972) determined that a period of rapid increase in clasper length indicates the onset of sexual maturity in male *S. acanthias*. A similar allometric growth phase between clasper length and TL was observed for *S. mitsukurii*. Thus, the right clasper length was measured to the nearest 1 mm from the body juncture to the clasper tip.

To determine the size at 50% sexual maturity for both sexes, data were fitted to the logistic function by using an iteratively weighted (i.e. inverse of variance) nonlinear estimation procedure (Wilkinson, 1988) and evaluated at 50% (Somerton, 1980). The logistic equation is defined as

$$Y = 1/(1 + Ae^{BX}),$$

where Y is the proportion of animals sexually mature, X is the midpoint of a length class, and A and B are parameters defining the curve. Before the logistic equation was fitted to length data for males, the data were transformed to approximate the logistic pattern of growth. For example, clasper length (CL) plotted against fish TL (not shown) produced a roughly sigmoid curve, although at large and small fish sizes, clasper length continues to increase with size of the fish. To flatten the ends of the curve as required by the logistic equation, clasper length was expressed as a proportion of fish TL and normalized to values between 1 and 0 (i.e. with a=CL/TL, the quantity $Y'=(a-a_{min})/(a_{max}-a_{min})$ was plotted against fish TL).

To obtain information on feeding habits, the stomach contents from 251 *S. mitsukurii* caught on longlines and 42 fish caught in gill nets during the summer of 1986 were examined. Longline-caught fish ranged from 20.6 to 79.5 cm TL (mean length $\bar{L}$ =50.4 cm) and gillnet-caught fish ranged from 49.5 to 78.9 cm TL ($\bar{L}$ =65.5 cm). Samples from the bottom longline and gillnet gear were compared to examine the potential feeding bias that might occur if attraction to baited longlines varied as a function of stomach fullness for *S. mitsukurii*.

For most of the fish, stomachs were extracted upon capture and preserved in 10% formalin until examination in the laboratory. However, if time permitted, stomachs were examined at sea for the presence of food items; empty stomachs were noted and discarded (those with food items were saved). In the laboratory, samples were sorted, counted, and identified to the lowest possible taxon. Food items were sorted to taxa, blotted dry, and weighed to the nearest 0.1 g.

Stomach contents data were analyzed for frequency of occurrence, numerical abundance, and gravimetric proportions of prey items to quantitatively describe the diet and feeding habits of *S. mitsukurii* (Hyslop, 1980). Prey items that were attributed to the presence of the research vessel (i.e. bait, galley refuse, or processed fish offal) were not included in the analyses; stomachs containing only those items were considered empty. To examine diel feeding behavior, samples were grouped by time of capture: 0600–1200 (n=39), 1200–1800 (n=86), 1800–2400 (n=64), and 0000–0600 (n=62). Chi-square (χ^2) analyses of 2 × 2 contingency tables were used to test for

differences in stomach fullness (defined simply in terms of presence versus absence of food) between time blocks. Sunrise was at about 0545 h and sunset at 1930 h. The χ^2 test was similarly used to identify differences in stomach fullness between longline- and gillnet-caught fish from a single time block (1800–2400 h).

Results

Abundance

A total of 1,392 female, 1,539 male, and 7 unsexed, hook-caught *S. mitsukurii* were collected. CPUE was highest in 1985 and declined by more than 50% by spring 1987 (Table 1). The CPUE data plotted as a function of cumulative catch (C) appeared generally linear with a negative slope (Fig. 2); coefficients of the fitted model were CPUE $= -6.87 \times 10^{-5} \times C + 0.2498$ (r^2=0.76). The model estimate of the initial exploitable population was 3,641 fish (±1,954). Based on this estimate, about 80% (±55%) of the initial population of *S. mitsukurii* had been removed by fishing.

Both sexes of *S. mitsukurii* were caught over the full depth range sampled. The median depth of occurrence for males was usually greater than that of females (Table 2).

Size

Female *S. mitsukurii* were on average longer and reached larger maximum sizes than males (Fig. 3). Maximum lengths recorded were 91 cm for females and 82 cm for males. Differences were also detected in length-weight data between female and male *S. mitsukurii* (ANCOVA, P<0.05). Nonlinear fits of length-weight growth curves between sexes diverged at about the size at 50% maturity for male sharks (see Reproduction). Length-weight parameter estimates were $a=1.718 \times 10^{-2}$, b=2.687 for males and $a=3.773 \times 10^{-3}$, b=3.089 for females.

The size of male sharks increased with depth. For example, for each cruise and sex, fish were divided into either a shallow or deep subgroup, depending on whether they were caught above or below the median depth of occurrence for that group on that cruise. Estimates of the median length for males from the deep group were

Table 2

Maximum and median depth (m) of occurrence for female and male *Squalus mitsukurii*, median length (cm) for each sex above and below median depth of occurrence, and statistical significance between median depths or lengths (Mann-Whitney U-test, *P≤0.05, **P≤0.001).

Sampling period	Sex	Maximum depth	Median depth	Median length above/below median depth
Winter 1985	F	443	302**	66.0/61.0
	M	459	327	59.9/58.7
Summer 1985	F	744	309*	58.4/50.0
	M	744	327	52.6/58.5*
Summer 1986	F	556	260*	41.8/45.6
	M	454	269	43.5/50.9**
Fall 1986	F	468	291*	54.4/51.2
	M	494	298	52.1/54.1
Spring 1987	F	384	293	48.9/47.9
	M	518	269	46.8/54.2
Summer 1987	F	483	283	43.2/45.4*
	M	459	283	40.5/46.2**
Winter 1988	F	512	272	50.3/56.0*
	M	446	276	52.2/58.6*
Summer 1988	F	569	411	50.2/52.3
	M	569	448	46.0/55.2**
Fall 1988	F	430	274	56.0/50.9
	M	382	278	50.0/52.2

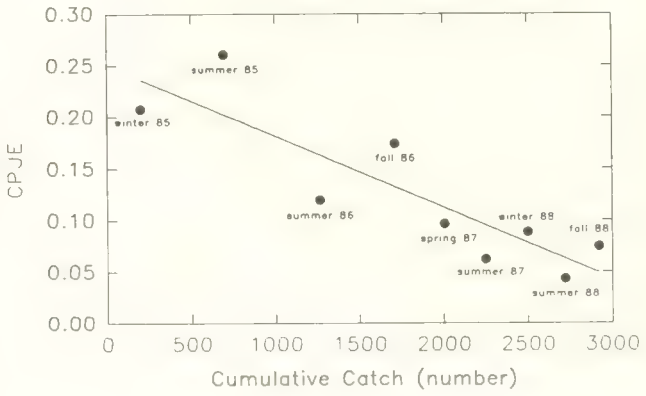

Figure 2

Catch per unit of effort (CPUE) for each sampling period (filled circles) and predicted CPUE based on the Leslie model (solid line), and plotted as a function of cumulative catch for *Squalus mitsukurii* from SE Hancock Seamount during 1985–88.

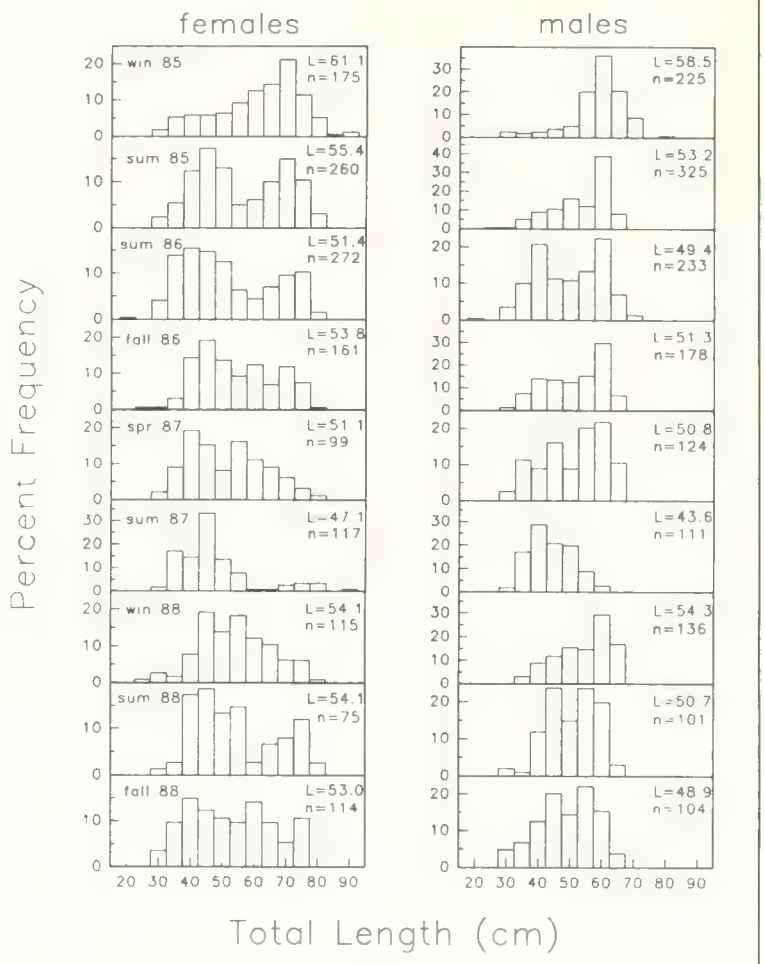

Figure 3

Size–frequency composition of female and male *Squalus mitsukurii* from cruises to SE Hancock Seamount during 1985–88. *L*=mean length.

significantly greater than for the shallow group on five of nine cruises (Mann-Whitney *U*-test, $P<0.05$) with similar, nonsignificant trends seen on three additional cruises (Table 2). These differences were greatest in summer. There was no apparent trend in size with depth for females (Table 2).

Age and growth

Spine increments were counted for 102 males (20.8–72.2 cm TL) and 105 females (20.6–79.5 cm TL). Increment counts ranged from 0 to 27 for female spines and 0 to 18 for male spines. Mean length at age for each sex was similar up to age 9; thereafter, females grew faster (Fig. 4). For both sexes, the mean length at time 0 was greater than that expected based on the estimated size at parturition for *S. mitsukurii* (see Reproduction).

Fitted growth curves for each sex differed considerably (Fig. 4). The L_∞ estimate for females exceeded the observed maximum length from the catch data (i.e. 91 cm), although the L_∞ estimate for males was much lower than the observed value of 82 cm.

Reproduction

Reproductive data were collected from a total of 258 female *S. mitsukurii* specimens during 1986–88. Gravid females examined during the four seasons ranged from 61 to 80 cm TL. The estimated size at 50% sexual maturity for females was 69 cm (Fig. 5). This size corresponds to an age of about 15 years. The largest infertile or sexually inactive female was 88 cm. No differences were found in the depth distributions of gravid and nongravid females greater than

60 cm in length (i.e. minimum observed size at maturity; Kolmogorov- Smirnov test, P=0.069).

Estimates of fecundity for female *S. mitsukurii* were similar regardless of the reproductive stage used. Gravid females had similar mean numbers of large ovarian eggs (3.8, SE=0.10, n=95), candled embryos (3.7, SE=0.15, n=40), and uterine embryos (3.6, SE=0.15, n=57); numbers for any developmental stage ranged from 1 to 6. Fecundity increased significantly with the size of the female (Table 3, Spearman's r=0.44, 0.40, 0.46; P<0.05).

The size range of uterine embryos (65 female, 51 male, and 73 unsexed) for *S. mitsukurii* was 6.6–25.9 cm TL ($\bar{L}$=17.8 cm, SD=5.57). A very large (30.5 cm TL) male embryo from winter 1988 was excluded because its length could not be verified. Bimodal size-frequency distributions of the uterine embryos were evident for samples from all periods (Fig. 6). All gravid females had one of two size classes of uterine embryos. Further, the total numbers of uterine embryos within all but fall 1988 samples were apportioned approximately equally between the "small" and "large" size classes (χ^2, P>0.05).

No well-defined parturition season was detected either from a large increase in catches of small (i.e. 21–26 cm), free-living fish (Fig. 3) or by the absence of large, near-term embryos in females (Fig. 6). However, the smallest uterine embryos were found in fall and winter and were absent in spring and summer (Fig. 6), which is indicative of a reasonably well-defined seasonal production cycle for young. Specimens as small as 21 cm were captured from longline gear in summer 1986. This confirms that 21–26 cm long embryos would be close to parturition. The only significant correlation between numbers of "large," "small," or total uterine embryos, candled embryos, or large ovarian eggs was a positive association between numbers of uterine embryos and large ovarian eggs (Pearson's r=0.62, P<0.05).

Size at sexual maturity for male *S. mitsukurii* was estimated indirectly from 812 specimens. The estimated size at 50% sexual maturity was 48 cm (Fig. 5). This corresponds to a tentative age of about 4 years based on the von Bertalanffy growth equation.

Feeding

Overall, 101 of the 293 (34.5%) stomachs examined contained prey. Stomach contents averaged 2.0 prey items (SD=1.4) and weighed 4.5 g (SD=9.3 g). Fishes, cephalopods, and crustaceans were the

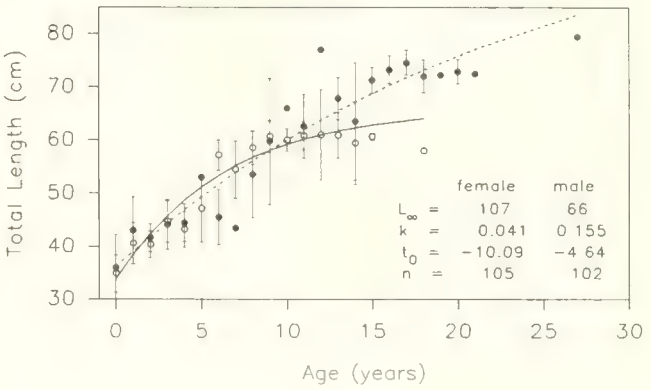

Figure 4

Fitted von Bertalanffy growth curves and mean length-at-spine increment counts for female (dashed line, filled circles) and male (solid line, open circles) *Squalus mitsukurii*. Vertical lines represent 95% confidence intervals. The von Bertalanffy growth parameters are defined in the text.

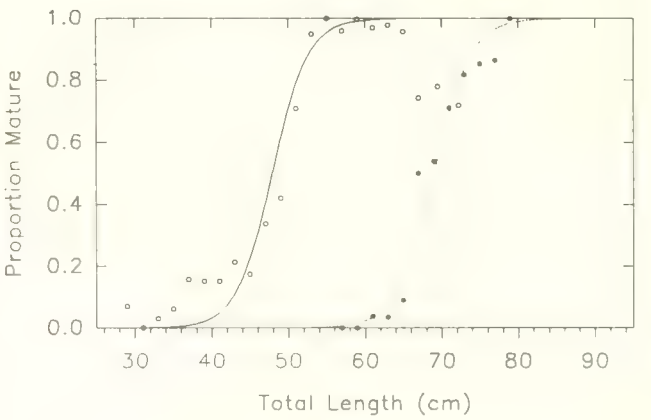

Figure 5

Fitted logistic function and proportion mature at each size-class for female (filled circles) and male (open circles) *Squalus mitsukurii*. Size class intervals are 2 cm. Points representing the three largest size classes for males appear as outliers but were not eliminated because few observations comprised these points (n=6, 1, 1). Thus we were uncertain whether they accurately represent the relationship between clasper and total length for large fish (which we had insufficient data to define) or whether the points were a result of measurement error. Regardless of whether these "extreme" values were removed or left in the data set, they had relatively little influence in fitting the function (see text).

Table 3

Mean length, standard deviation (SD), and number of gravid *Squalus mitsukurii* specimens as a function of number of large ovarian eggs and candled and uterine embryos.

Maternal statistics	Number of eggs or candled or uterine embryos					
	1	2	3	4	5	6
Large ovarian eggs						
Mean length	68.0	71.1	70.1	72.3	74.4	75.1
SD	—	2.49	3.97	2.96	3.18	2.91
Number	1	4	33	35	18	4
Candled embryos						
Mean length	70.5	74.6	72.0	74.0	76.1	76.2
SD	—	5.30	4.03	2.17	2.58	—
Number	1	2	14	17	5	1
Uterine embryos						
Mean length	73.1	68.1	72.4	74.4	76.1	79.5
SD	3.76	1.63	3.89	2.24	2.09	–
Number	4	2	21	18	11	1

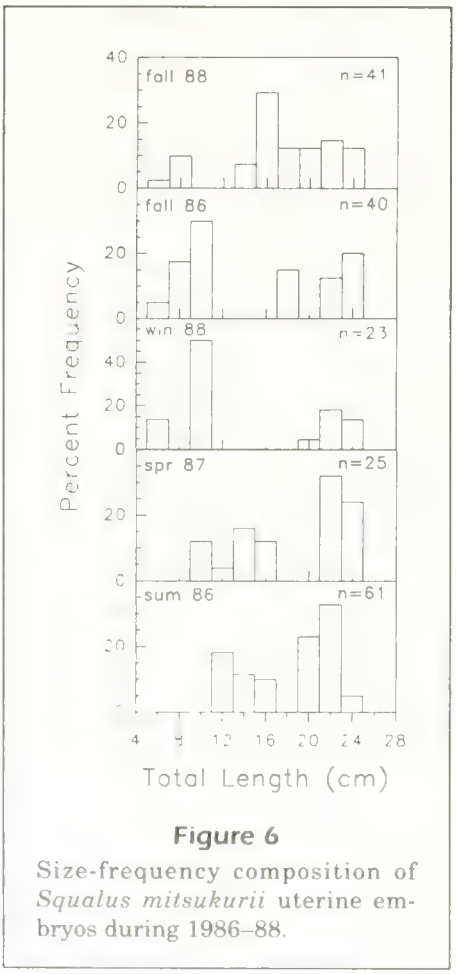

Figure 6

Size-frequency composition of *Squalus mitsukurii* uterine embryos during 1986–88.

major components of the diet (Table 4). Fishes were found in 63.7% of the stomachs with prey and numerically accounted for 36.8% of the total prey while making up 74.5% of the total aggregate weight. Micronektonic stomiiform and myctophid fishes, and filefishes (family Monacanthidae) were the most commonly identified fishes; however, most fishes were in an advanced stage of digestion and thus unidentifiable to a lower taxon. Crustaceans were present in 32.3% of the stomachs and represented 30.3% of the prey organisms, but only 3.6% of the total aggregate weight. In particular, euphausiids and the lophogastrid mysid *Gnathophausia longispina*, were commonly found. Cephalopods, predominantly digestion-resistant squid beaks and eye lenses, were present in 45.1% of the stomachs, representing 26.4% of the total prey items and 19.9% of the prey weight. Remaining prey items included pelagic tunicates, coelenterates, and unidentified remains.

Gut fullness was evaluated as a function of diel feeding activity and gear type. For longline data, no significant difference was found between the two daytime (χ^2=0.001, P>0.1) or two nighttime blocks (χ^2=3.822, P>0.1). However, when longline data from daytime blocks were pooled and compared with pooled nighttime blocks, the proportion of empty stomachs was significantly greater during the night (87%) than during the day (46%; χ^2=26.250, P<0.001). Longline-caught fish had a significantly greater proportion of empty stomachs than did fish caught by bottom gill net (χ^2=5.081, P<0.05).

Discussion

Size and abundance

Squalus mitsukurii was the second most abundant species sampled by bottom longline gear at SE Hancock Seamount in 1985–88 (Somerton[4]). However, the large apparent decline in catch rates for *S. mitsukurii* during this period suggests that the research fishing may have had a major impact on stock size which is (i.e. in 1988) at only 20% of its 1985 value. It is likely that populations of this species, like other elasmobranchs (Holden, 1974), are particularly sensitive to overfishing. In addition, seamount populations of *S. mitsukurii* may be at further risk to overexploitation because of the limited habitat

[4] Somerton, D. National Marine Fisheries Service, Seattle, WA 98115. Personal commun., 1992.

Table 4

Diet composition (as identified to lowest possible taxon) for 101 *Squalus mitsukurii* at SE Hancock Seamount.

Taxa	Total no.	% no.	Total weight (g)	% weight	Frequency	% frequency
Coelenterata	1	0.5	0.5	0.1	1	1.0
Cephalopoda	41	20.7	11.2	2.5	35	34.6
Sepiolidae	2	1.0	7.5	1.7	2	2.0
Iridoteuthis iris	1	0.5	2.1	0.5	1	1.0
Histioteuthidae	1	0.5	1.1	0.2	1	1.0
Enoploteuthidae						
Enoploteuthis sp.	1	0.5	25.0	5.5	1	1.0
Ommastrephidae	5	2.5	22.5	5.0	5	4.9
Octopoda	3	1.5	21.0	4.6	3	3.0
Crustacea	2	1.0	1.5	0.3	1	1.0
Mysidacea						
Gnathophausia longispina	13	6.6	1.9	0.4	10	9.9
Amphipoda						
Phronima sp.	1	0.5	0.3	0.1	1	1.0
Euphausiacea	11	5.6	0.8	0.2	6	5.9
Thysanopoda aequalis	1	0.5	0.1	<0.1	1	1.0
Thysanopoda sp.	17	8.6	1.6	0.3	8	7.9
Euphausia gibboides	1	0.5	0.1	<0.1	1	1.0
Euphausia sp.	2	1.0	0.2	<0.1	2	2.0
Decapoda						
Sergestidae	7	3.5	1.1	0.2	7	6.9
Penaeidae						
Gennadas propinquus	1	0.5	0.1	<0.1	1	1.0
Gennadas tinayrei	1	0.5	0.1	<0.1	1	1.0
Gennadas sp.	2	1.0	0.4	0.1	2	2.0
Caridea	1	0.5	5.0	1.1	1	1.0
Oplophoridae	1	0.5	0.1	<0.1	1	1.0
Reptantia	1	0.5	3.0	0.7	1	1.0
Pisces	39	19.7	83.3	18.4	38	37.6
Leptocephalus	1	0.5	1.5	0.3	1	1.0
Stomiiformes	5	2.5	12.5	2.8	5	4.9
Sternoptychidae						
Maurolicus muelleri	1	0.5	1.3	0.3	1	1.0
Melanostomiidae	3	1.5	57.3	12.7	3	3.0
Aulopiformes						
Paralepididae	1	0.5	0.3	0.1	1	1.0
Myctophiformes						
Myctophidae	4	2.0	9.5	2.1	4	4.0
Lampanyctus sp.	1	0.5	13.0	2.9	1	1.0
Beryciformes						
Berycidae						
Beryx splendens	1	0.5	56.4	12.5	1	1.0
Perciformes						
Apogonidae						
Epigonus sp.	2	1.0	4.3	0.9	2	2.0
Callanthiidae						
Grammatonotus laysanus	2	1.0	59.9	13.2	2	2.0
Echeneidae	1	0.5	2.1	0.5	1	1.0
Emmelichthyidae	2	1.0	32.2	7.1	2	2.0
Pleuronectiformes						
Bothidae	1	0.5	0 7	0.1	1	1.0
Tetraodontiformes						
Monacanthidae	11	5.6	4.5	1.0	8	7.9
Tunicata						
Pyrosomatidae						
Pyrosoma sp.	3	1.5	3.2	0.7	3	3.0
Salpidae	1	0.5	0.1	<0.1	1	1.0
Unidentified remains	8	4.0	5.4	1.2	8	7.9

area. In the case of SE Hancock Seamount, for example, the summit diameter is only about 2.4 km. Assuming recruitment is entirely dependent on the seamount population (i.e. little or no immigration from elsewhere), relatively little fishing effort is required to seriously deplete the stock.

It is not possible to verify whether the assumptions that are required by the Leslie model were met in the present study. The model assumes that changes in population abundance (i.e. CPUE) are due to fishing removals whereas other losses such as emigration and natural mortality are balanced by additions such as immigration and recruitment of young to the exploited population. The model has generally been applied over shorter time periods in other studies where the assumptions are more readily satisfied (Polovina, 1986; Somerton and Kikkawa, 1992). The fact that our model data were taken over a period of about four years may have introduced some noise into the results. Nevertheless, studies have indicated that members of the genus *Squalus* do exhibit low levels of natural mortality (Wood et al., 1979) and fecundity (see Reproduction below). Whether *S. mitsukurii* move among seamounts is unknown. Unfortunately, results from tagging studies with *S. acanthias* (McFarlane and Beamish, 1986 and references therein) are of limited usefulness to our work since they were not conducted over relatively isolated seamounts found in deep oceanic waters. However, tagging work on *S. acanthias* within the Strait of Georgia suggests that most recoveries were made within the areas of release although some long distance movements were also recorded (McFarlane and Beamish, 1986). Thus, while our application of the Leslie model to data taken over a period of several years may be somewhat unusual, there is no existing evidence that invalidates our assumption that the losses and additions to the seamount shark population were generally in balance over this time period.

Bottom longlines rather than trawls were the primary sampling gear used during the NMFS surveys. The few numbers of *S. mitsukurii* taken earlier in the commercial trawl fishery (Sasaki[5]) may have been the result of the different gear types. Other studies have reported the reduced effectiveness of trawls, relative to bottom longline gear, in catching *S. mitsukurii* (Litvinov, 1990).

The decreasing catch rates of *S. mitsukurii* at SE Hancock Seamount suggest a decline in the population size. However, a concomitant decrease in mean length was not observed for either sex (Fig. 3). This may have occurred because there were large removals from the population with little or no recruitment from smaller (younger) size classes. It is interesting that no size class(es) appeared to progress through the population during the period of study.

Little has been reported concerning the bathymetric distribution patterns of *S. mitsukurii* from other regions. Although *S. mitsukurii* at the seamount and in other regions have a similar maximum depth of occurrence (Compagno, 1984), it is unknown whether *S. mitsukurii* females and males from other populations exhibit depth distributions similar to those at SE Hancock Seamount (Table 2). Sexes of the closely related species *S. acanthias* generally show the opposite trend; males were found at shallower depths than were females (Compagno, 1984).

The largest specimens of *S. mitsukurii* from our study attained sizes similar to the maximum generally reported for other areas. Off South Africa, maximum lengths for *S. mitsukurii* of 81 cm for males and 95 cm for females were reported by Bass et al. (1976). The maximum size we report agrees with that from an earlier study (Taniuchi et al., 1993) at SE Hancock (88–92 cm; n=72 specimens) but not that from another locality in the western North Pacific (112–116 cm).

Age and growth

Unvalidated estimates of age based on the second dorsal spine increment counts from 63 fish have been reported for *S. mitsukurii* from the SE Pacific Ocean (Litvinov, 1990). In that study, the maximum age for males was 14 years and for females was 16 years. In the present study maximum ages were somewhat higher: 18 years for males and 27 years for females.

Although tentative, our estimates of age based on spine increment counts suggest that *S. mitsukurii*, like *S. acanthias* (McFarlane and Beamish, 1987), is long-lived. However, maximum ages for *S. mitsukurii* were generally less than those for *S. acanthias*. Maximum ages for *S. acanthias* are quite variable. In the NE Pacific Ocean, ages may exceed 80 years (McFarlane and Beamish, 1987), in the Atlantic Ocean, ages to 40 years have been reported (Nammack et al., 1985), and in the Black Sea, maximum ages may be only 20 years (Kirnosova, 1989). Whether *S. mitsukurii* is a shorter-lived species than *S. acanthias* will require the evaluation of additional samples. Fishing on *S. mitsukurii* at SE Hancock Seamount may have removed much of the older segment of the population before we collected our age sample in the summer of 1986. Thus, the largest fish we aged was only 80 cm, whereas the largest fish caught was 91 cm. This suggests that *S. mitsukurii* may live longer.

[5] Sasaki, T. National Research Institute of Far Seas Fisheries, Shimizu, Japan. Personal commun., 1992.

The von Bertalanffy growth model was fit to age-length data for *S. mitsukurii*. Increases in $\bar{L}$ with age occurred for both sexes, although few larger, presumably older, specimens in the age sample may have prevented a reliable evaluation of growth over the entire age spectrum. Nonetheless, the growth model seemed to represent observed patterns fairly well over younger ages and smaller sizes for each sex. Rather perplexing is the fact that observed and predicted $\bar{L}$ values at age 0 (Fig. 4) were larger than the observed size at parturition (see below). Possibly the birth of age-0 fish occurs at times other than when our age sample was taken (August–September). If this is the case, the formation of the first increment may not have occurred although the fish had grown in length. Alternatively, young-of-the-year fish may not lay down an increment until their second winter, or we may have simply missed the first increment which is often poorly defined, as with *S. acanthias* (Saunders[6]).

Reproduction

Our results provide some insight into the gestation period for *S. mitsukurii*. The bimodal uterine size distributions that we observed during all seasons, and which exhibited no clearly dominant mode, are consistent with the two-year gestation period of the closely related species *S. acanthias* (Compagno, 1984; Ketchen, 1986; but see Kirnosova, 1989). To confirm the gestation period, however, information is needed on the growth rate of uterine embryos and the time required for the smaller size class to replace the larger size class.

Slight differences in reproductive traits of *S. mitsukurii* were detected between specimens collected at SE Hancock Seamount and from other areas. The minimum size at sexual maturity was 65 cm for females and 55 cm for males off South Africa (Bass et al., 1976), which was similar for females but larger than that of males (<48 cm) in our study. Only the female minimum size at maturity (85 cm) was reported for the SE Pacific (Litvinov, 1990). The value exceeded that of our study. In the North Pacific, Taniuchi et al. (1993) reported larger minimum lengths at maturity for both sexes than those reported here. Their reported minimum lengths at maturity, which included data from 72 fish from SE Hancock Seamount and which were expressed in 4-cm intervals, ranged from 68–72 cm to 96–99 cm for females and 48–52 cm to 68–72 cm for males.

Length and age at maturity for male *S. acanthias* are relatively high in the North Pacific (e.g. 72 cm, 14 years; Ketchen, 1975) compared with other areas, such as the Northwest Atlantic (e.g. 60 cm, 6 years; Nammack et al., 1985) and South Pacific (e.g. 58 cm, 6 years; Hanchet, 1986). For *S. mitsukurii* males from the central North Pacific, however, our estimated age at maturity is quite low (ca. four years). Thus, unlike *S. acanthias*, it seems doubtful that younger ages at maturity will be found in other regions (e.g. South Pacific), assuming our preliminary estimates of age are not seriously in error.

There were no apparent geographical differences in fecundity for *S. mitsukurii*. The reported number of large ovarian eggs (two to five) for females in the southeast Pacific (Litvinov, 1990) agrees with our study. A mean of 6.4 embryos per gravid female (range, 4–10) was reported off southeast Africa (Bass et al., 1976) compared with 3.6 from our study. However, the data from South Africa were taken from larger (76–95 cm) females. Likewise, litter sizes ranged from 2 to 15 (present study 1–6) from relatively large specimens collected in the western North Pacific (Taniuchi et al., 1993). When compared over sizes similar to those in the present study, however, litter sizes were nearly identical (2–6 versus 1–6). Thus, it is probable that the difference between our results and the latter two studies can be attributed to the positive relationship between parent length and fecundity reported in our study (Table 3) and by Taniuchi et al. (1993).

The lengths of near-term embryos from the South African specimens were at least 22 cm (Bass et al., 1976), and those from the southeast Pacific were 29–30 cm (Litvinov, 1990). Although our estimated near-term embryo lengths were similar to those from South Africa, those from the southeast Pacific were larger, possibly because of a positive relationship between the length of the parent and those of the near-term embryos.

Feeding

Squalus mitsukurii fed on a variety of benthic and particularly mesopelagic fishes, crustaceans, and cephalopods at SE Hancock Seamount. Other diet studies have also concluded that *S. mitsukurii* consume a variety of prey types. In the Indian Ocean, for example, *S. mitsukurii* consumed teleosts (57%), cephalopods (33%), and crustaceans (10%) (Bass et al., 1976). On seamounts in the Southeast Pacific, prey included fishes, crustaceans, and cephalopods (Litvinov, 1990). Along the west coast of South Africa, a species tentatively described as *S. mitsukurii* fed predominately on fishes and cephalopods (Ebert et al., 1992).

[6] Saunders, M. Pacific Biological Station, Nanaimo, B.C. Personal commun., 1991.

In diet studies of the related temperate species *S. acanthias* (Bonham, 1954; Holden, 1966; Jones and Geen, 1977), consumed prey diversity was often lower than that of *S. mitsukurii* at SE Hancock with a large variation in the dominant prey species by season and location. These studies typically found that *S. acanthias* feed on the most abundant prey items available (normally teleost fishes), although other pelagic organisms (primarily euphausiids) were important, particularly for smaller sharks (Jones and Geen, 1977). *Squalus acanthias* often inhabit shelf areas that may maintain large influxes of a few different pelagic species that opportunistic predators such as squalids can exploit (Brodeur and Pearcy, 1992). *Squalus mitsukurii* at SE Hancock Seamount fed on a great diversity of mesopelagic prey typical of oceanic environments (Boehlert and Genin, 1987; Reid et al., 1991).

Because *S. mitsukurii* specimens in our feeding study were taken from gear set on the bottom, finding benthic prey, such as pleuronectiforms, crabs, or octopods, in the diet was not surprising. Based on results from our vertical longline sets and midwater trawling, however, *S. mitsukurii* did not appear to move high enough above the summit to feed on mesopelagic prey. Rather, these prey species (e.g. stomiiform fishes, lophogastrid mysids) were likely consumed by *S. mitsukurii* as the fauna were advected over or around the seamount. A similar mechanism may exist for other resident fish predators at SE Hancock (Seki and Somerton, 1994). Various studies have documented the importance of current-topographical interactions to biological processes in these environments (reviewed in Boehlert and Genin, 1987), as well as the exploitation of oceanic prey species by demersal predators as the former are advected over banks (Isaacs and Schwartzlose, 1965; Genin et al., 1988) or concentrate in submarine canyons (Pereyra et al., 1969). Over other seamounts, mesopelagic micronekton prey have been found to be an important, if not principal, forage base for resident fish populations (Parin and Prut'ko, 1985).

A high proportion of *S. mitsukurii* stomachs were classified as empty in our study (65%). The occurrence of numerous empty stomachs for squalid species has often been attributed to a combination of intermittent feeding behavior and partial regurgitation of food items (Bonham, 1954; Holden, 1966; Bowman, 1986). Whether the use of hook-and-line gear is biased towards actively feeding fish with empty stomachs is unknown. Holden (1966) discounted this hypothesis after he found a greater proportion of empty guts from trawl-caught rather than line-caught *S. acanthias*. However, the greater frequency of empty stomachs from longline-caught rather than gillnet-caught fish in our study suggest further consideration of this hypothesis. It is possible that the rapid recovery of longlines to the surface may have increased the likelihood of food regurgitation or stomach flushing. However, we did not observe direct evidence of regurgitation, although the high frequency of empty stomachs filled with water suggests that undetected regurgitation may have occurred (see Bowman, 1986). Whether the preponderance of empty guts in this study actually reflects some aspect of feeding behavior or is simply an artifact of the sampling process requires further work.

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Literature cited

Bass, A. J., J. D. D'Aubrey, and N. Kistanasamy.
1976. Sharks of the east coast of southern Africa. VI: The families Oxynotidae, Squalidae, Dalatiidae, and Echinorhinidae. Invest. Rep. Oceanogr. Res. Inst. 45:1–103.

Bass, A. J., L. J. V. Compagno, and P. C. Heemstra.
1986. Squalidae. *In* M. M. Smith and P. C. Heemstra (eds.), Smiths' sea fishes, p. 49–62. Springer-Verlag, Berlin.

Beamish, R. J., and G. A. McFarlane.
1985. Annulus development on the second dorsal spine of the spiny dogfish (*Squalus acanthias*) and its validity for age determination. Can. J. Fish. Aquat. Sci. 42:1799–1805.

Boehlert, G. W., and A. Genin.
1987. A review of the effects of seamounts on biological processes. *In* B. H. Keating, P. Fryer, R. Batiza, and G. W. Boehlert (eds.), Seamounts, islands, and atolls, p. 319–334. Geophys. Monogr. 43 (Am. Geophys. Union).

Bonham, K.
1954. Food of the dogfish *Squalus acanthias*. Wash. Dep. Fish., Fish. Res. Pap. 1:25–36.

Bowman, R. E.
1986. Effect on regurgitation on stomach content data of marine fishes. Environ. Biol. Fishes 16:171–181.

Brainard, R. E.
1986. Fisheries aspects of seamounts and Taylor columns. M.S. thesis, Naval Postgraduate School, Monterey, CA, 88 p.

Brodeur, R. D., and W. G. Pearcy.
1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic

upwelling ecosystem. Mar. Ecol. Prog. Ser. 84:101–119.

Compagno, L. V. J.
1984. FAO species catalogue. Vol. 4: Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1: Hexanchiformes to Lamniformes. FAO Fish. Synop. 125, 249 p.

Ebert, D. A., L. J. V. Compagno, and P. D. Cowley.
1992. A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of southern Africa. S. Afr. J. Mar. Sci. 12:601–609.

Genin, A., L. Haury, and P. Greenblatt.
1988. Interactions of migrating zooplankton with shallow topography: predation by rockfishes and intensification of patchiness. Deep-Sea Res. 35:151–175.

Hanchet, S. M.
1986. The distribution and abundance, reproduction, growth, and life history characteristics of the spiny dogfish, *Squalus acanthias* (Linnaeus) in New Zealand. Ph.D. thesis, Univ. of Otago, Dunedin, New Zealand, 292 p.
1988. Reproductive biology of *Squalus acanthias* from the east coast, South Island, New Zealand. N.Z J. Mar. Freshwater Res. 22:537–549.

Holden, M. J.
1966. The food of the spurdog, *Squalus acanthias*. J. Cons. Int. Explor. Mer 30:255–266.
1974. Problems in the rational exploitation of elasmobranch populations and some suggested solutions. *In* F. R. Harden-Jones (ed.), Sea fisheries research, p. 117–137. Halsted Press, New York, NY.

Holden, M. J., and P. S. Meadows.
1962. The structure of the spine of the spur dogfish (*Squalus acanthias* L.) and its use for age determination. J. Mar. Biol. Assoc. UK 42:179–197.

Hyslop, E. J.
1980. Stomach contents analysis—a review of methods and their application. J. Fish Biol. 17:411–429.

Isaacs, J. D., and R. A. Schwartzlose.
1965. Migrant sound scatterers: interactions with the sea floor. Science (Wash., D.C.) 150:1810–1813.

Jones, B. C., and G. H. Geen.
1977. Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Board Can. 34:2067–2078.

Ketchen, K. S.
1972. Size at maturity fecundity and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Board Can. 29:1717–1723.
1975. Age and growth of dogfish *Squalus acanthias* in British Columbia waters. J. Fish. Res. Board Can. 32:43–59.
1986. The spiny dogfish (*Squalus acanthias*) in the northeast Pacific and a history of its utilization. Can. Spec. Publ. Fish. Aquat. Sci. 88, 78 p.

Kirnosova, I. P.
1989. Reproduction of spiny dogfish, *Squalus acanthias* in the Black Sea. J. Ichthyol. 29:21–26.

Litvinov, F. F.
1990. Ecological characteristics of the dogfish, *Squalus mitsukurii* from the Sala-y-Gomez Seamounts. J. Ichthyol. 30:104–115.

McFarlane, G. A., and R. J. Beamish.
1986. A tag suitable for assessing long-term movements of spiny dogfish and preliminary results from use of this tag. N. Am. J. Fish. Manage. 6:69–76.
1987. Validation of the dorsal spine method of age determination for the spiny dogfish. *In* R. C. Summerfelt and G. E. Hall (eds.), The age and growth of fish, p. 287–300. Iowa State Univ. Press, Ames, IA.

Nammack, M. F., J. A. Musick, and J. A. Colvocoresses.
1985. Life history of spiny dogfish off the northeastern United States. Trans. Am. Fish. Soc. 114:367–376.

NMFS (National Marine Fisheries Service).
1986. Western Pacific bottomfish and seamount groundfish fisheries. Rules and regulations, 50 CFR Part 683. Federal Register 51(147):27413–27419.

Parin, N. V.
1987. Species of spiny dogfish of genus *Squalus*, living on southeastern Pacific Ocean seamounts. J. Ichthyol. 27(5): 43–50.

Parin, N. V., and V. G. Prut'ko.
1985. The thalassial mesobenthopelagic ichthyocoene above the Equator Seamount in the western tropical Indian Ocean. Oceanology 25:781–783.

Pereyra, W. T., W. G. Pearcy, and F. E. Carvey Jr.
1969. *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Board Can. 26:2211– 2215.

Polovina, J. J.
1986. A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock. Fish. Bull. 84:423–428.

Reid, S. B., J. Hirota, R. E. Young, and L. E. Hallacher.
1991. Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. Mar. Biol. 109:427–440.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

Seki, M. P., and D. A. Somerton.
1994. Feeding ecology and daily ration of the pelagic armorhead, *Pseudopentaceros wheeleri*, at SE Hancock Seamount. Environ. Biol. Fishes, 39:73–84.

Somerton, D. A.
1980. A computer technique for estimating the size of sexual maturity in crabs. Can. J. Fish. Aquat. Sci. 37:1488–1494.

Somerton, D. A., and B. S. Kikkawa.
1992. Population dynamics of pelagic armorhead *Pseudopentaceros wheeleri* on SE Hancock Seamount. Fish. Bull. 90:756–769.

Taniuchi, T., T. Hiroyuki, and M. Shimizu.
1993. Geographical variations in reproductive parameters of shortspine spurdog in the North Pacific. Nippon Suisan Gakkaishi 59:45–51.

Tucker, R.
1985. Age validation studies on the spines of the spurdog (*Squalus acanthias*) using tetracycline. J. Mar. Biol. Assoc. U.K. 65:641–651.

Uchida, R. N., and D. T. Tagami.
1984. Groundfish fisheries and research in the vicinity of seamounts in the North Pacific Ocean. Mar. Fish. Rev. 46(1):1–17.

Wilkinson, L.
1988. SYSTAT: The system for statistics. SYSTAT, Inc. Evanston, IL, 822 p.

Wood, C. C., K. S. Ketchen, and R. J. Beamish.
1979. Population dynamics of spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Board Can. 36:647–656.

Measures of dispersion as constraints for length-frequency analysis

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Length-frequency analysis (LFA) methods are widely used in population dynamics studies, particularly for tropical fish species that may be difficult or impossible to age by the traditional methods of reading growth rings on hard parts. LFA is characteristically subjective, and numerous authors have warned against its indiscriminate use, pointing out that estimated parameters may be questionable or even meaningless if the biology of the species is not taken into consideration or if the sampling was inadequate (e.g. Castro and Erzini, 1987; Macdonald, 1987; Morgan, 1987; Basson et al., 1988; Erzini, 1990). Biological information can be incorporated into these studies to obtain better results by using aged subsamples, time series of length-frequency distributions, or by constraining parameters to be estimated (Macdonald, 1987; Morgan, 1987). Constraints are based on assumptions concerning mortality, the relative abundance of the component age classes, the type of growth pattern or growth curve, the shape of the length-at-age distributions, the magnitude of the variability in length at age, and the pattern of this variability with age or size.

Our objective was to develop simple models, relating variability in length at age to life history and environmental parameters that could be used to select appropriate starting values and constraints for length-frequency analysis. We assumed that both the magnitude of variability in length-at-age and the size-and-age-dependent trends are related to species-specific life history and environmental characteristics. We demonstrate that measures of dispersion for particular lengths can be estimated on the basis of easily estimated parameter(s).

Methods

The data set used in this study consisted of 468 records representing 168 species and 50 families (Erzini, 1991). The following measures of variability in length at age were calculated: standard deviation of mean length at age (SD), variance of mean length at age (V), and coefficient of variation of mean length at age (CV). The following life history and environmental parameters were also compiled: von Bertalanffy K and L_∞, the Gallucci and Quinn (1979) growth parameter ω (intrinsic rate of growth), the growth performance index ϕ' (Longhurst and Pauly, 1987), maximum observed age, age at $0.95\,L_\infty$, spawning pattern, spawning duration (months), geographic location, and environmental regime (tropical, temperate, and boreal). Spawning patterns were described as continuous, continuous with one major peak, continuous with two peaks, discrete with one peak, and discrete with two peaks. Only data sets that were not based on LFA, composite samples, or back-calculated lengths at age were included in the analysis.

Stepwise multiple regression with selection of variables by maximum R^2 improvement (SAS Institute Inc., 1985) was used to evaluate the relative effectiveness of life history and environmental parameters in predicting three measures of dispersion (SD, V, and CV). Qualitative variables such as environmental regime and spawning pattern were represented by indicator variables with values of 0 and 1 (Neter et al., 1983). For each qualitative variable consisting of m classes, $m-1$ indicator variables were formed. Preliminary plots and simple and quadratic regressions were used to guide the transformation and creation of new variables, such as mean length at age squared for the stepwise regression, resulting in a total of 19 independent variables. Only data where the sample size corresponding to the measures of dispersion was at least 10 were used.

After multiple linear regression was used to identify the most important explanatory variables, simple linear regression was used to examine the trends in variability in length at age for data grouped into discrete classes of these variables. Three-dimensional smoothed plots of measures of dispersion as functions of the independent variables and the classification parameters were also used to investigate trends in variability in length at age.

Results

The multiple regression models show that the SD models have the highest R^2 values whereas the CV models have the lowest (Tables 1–3). The SD and the V are strongly influenced by size and certain

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growth parameters such as ϕ', ω, and L_∞. In the case of the CV, relative length at age seems to be the most important variable and the growth parameter variables were not selected for the models with five or less variables. Models with more than five independent variables are not shown as there was little further improvement in the amount of variation explained.

The influence of growth parameters can be seen in three-dimensional smoothed plots of the SD against relative length and L_∞ (Fig. 1), the SD against relative length and ϕ' (Fig. 2), and the SD against relative length and ω (Fig. 3). Magnitude of the variability of mean length at age generally increases with L_∞, ϕ', and ω. In contrast, no growth-parameter-related trends were found in plots involving CV. For example, in the plot of CV against relative length and K (Fig. 4), relative variability consistently decreased with size for all values of K.

Coefficent of variation and variation in CV decreased with increased relative length in all regressions for

Table 1

Examples of multiple linear regression models with the SD as the independent variable (n=3,050). ϕ' is the growth performance index, L_i is mean length-at-age, L_i^2 is the square of L_i, RL is relative length (L_i/L_∞), A_{95} is the age corresponding to $0.95L_\infty$ and ω is the Gallucci and Quinn (1979) growth parameter. MSE = the mean square error.

Model	MSE	R^2
$SD = -7.341 + 3.642\phi'$	1.99	0.62
$SD = -4.769 + 2.415\phi' + 0.022L_i$	1.66	0.68
$SD = -2.739 + 1.952\phi' + 0.028L_i - 1.479RL$	1.59	0.07
$SD = -3.532 - 0.049A_{95} + 0.092L_i - 4.280RL - 0.0002L_i^2$	1.49	0.72
$SD = 2.771 - 0.037A_{95} + 0.085L_i - 3.922RL - 0.0002L_i^2 + 0.023\omega$	1.47	0.72

Table 2

Examples of multiple linear regression models with the V as the independent variable (n=3,050). L_i is mean length at age, RL is relative length (L_i/L_∞), A is age, A_{95} is the age corresponding to $0.95L_\infty$, ω is the Gallucci and Quinn (1979) growth parameter, L_∞ is the von Bertalanffy growth parameter. MSE = the mean square error.

Model	MSE	R^2
$V = -6.314 + 0.0478L_i$	243.62	0.58
$V = -2.798 + 0.576L_i - 1.516A$	224.42	0.61
$V = 2.582 + 0.421L_i - 19.33RL + 0.464\omega$	216.45	0.62
$V = 1.198 + 0.472L_i - 16.80RL + 0.379\omega - 0.032A^2$	213.94	0.63
$V = 7.587 + 0.434L_i - 17.16RL - 0.025A^2 - 0.383A_{95} + 0.098L_\infty$	211.12	0.63

Table 3

Examples of multiple linear regression models with the CV as the independent variable (n=3,050). RL is relative length (L_i/L_∞), A is age, A_{95} is the age corresponding to $0.95L_\infty$, AA_{95} is age divided by A_{95}, and $AMAXA$ is age divided by the maximum observed age. MSE = the mean square error.

Model	MSE	R^2
$CV = 16.38 - 12.96RL$	16.50	0.31
$CV = 22.09 - 17.36RL - 0.171A_{95}$	13.95	0.42
$CV = 23.39 - 21.32RL - 0.173A_{95} + 3.614AA_{95}$	13.56	0.44
$CV = 22.97 - 19.97RL - 2.34AMAXA + 4.34AA_{95} - 0.155A_{95}$	13.41	0.44
$CV = 23.55 - 20.53RL - 2.411AMAXA + 3.49AA_{95} - 0.179A_{95} + 0.11A$	13.36	0.45

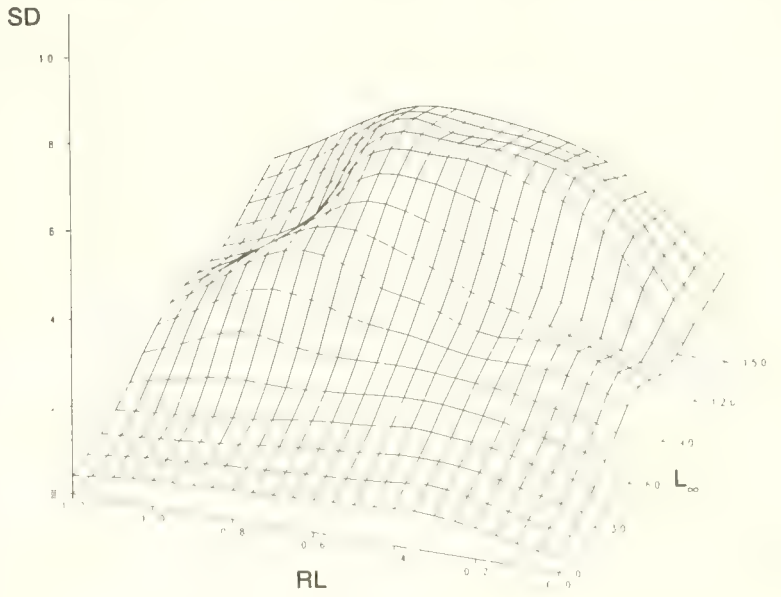

Figure 1

Smoothed surface graph of the standard deviation (SD) of mean length at age as a function of relative length (RL) and the asymptotic maximum length L_∞.

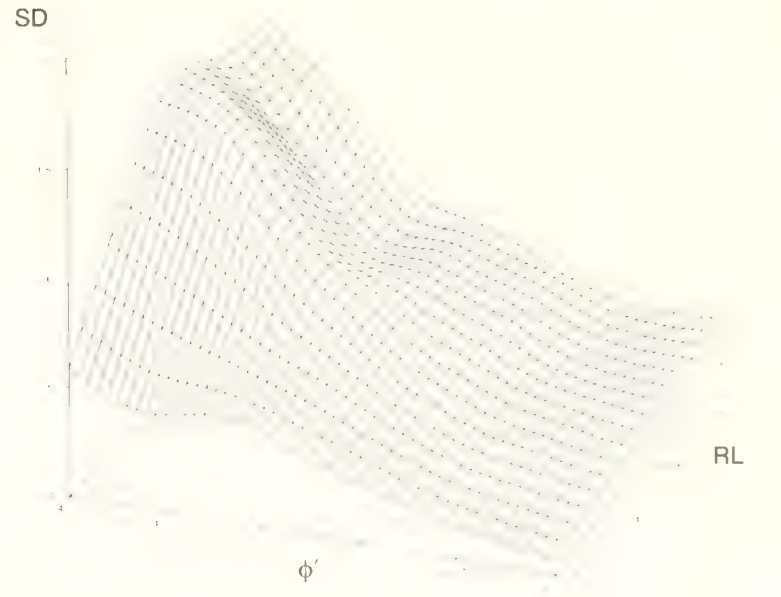

Figure 2

Smoothed surface graph of the standard deviation (SD) of mean length at age as a function of relative length (RL) and the growth performance index ϕ'.

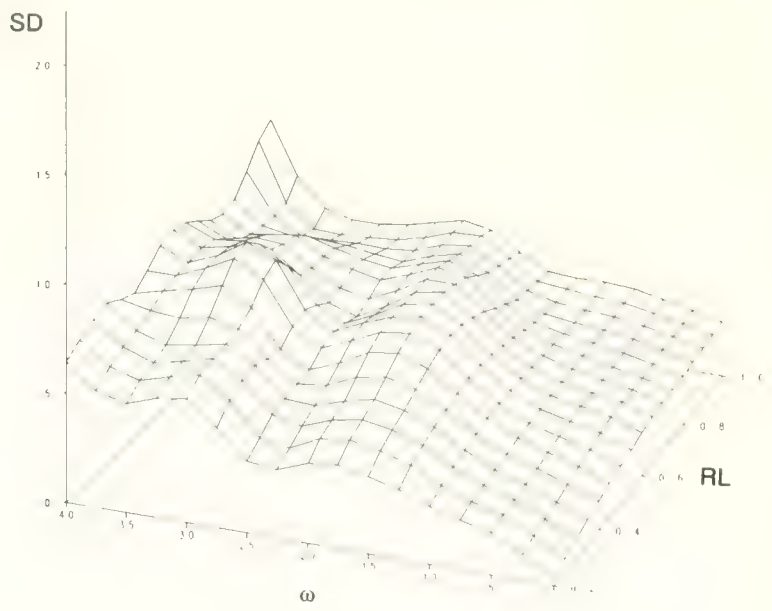

Figure 3

Smoothed surface graph of the standard deviation (SD) of mean length at age as a function of relative length and the parameter ω. (Gallucci and Quinn [1979] growth parameter.)

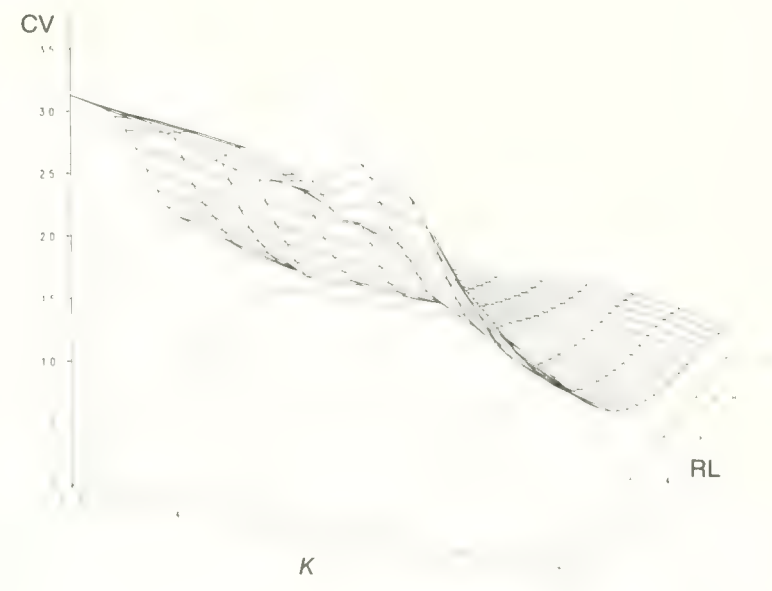

Figure 4

Smoothed surface graph of the coefficient of variation (CV) of mean length at age as a function of relative length (RL) and K, the growth rate.

Table 4

Regressions of the coefficient of variation (CV) against relative length (RL) for data grouped by the growth parameter.

	K	Intercept	Slope	n	MSE	R^2	P
a	0.05–0.099	13.39	–12.51	326	11.49	0.31	0.0001
b	0.10–0.149	15.51	–14.04	611	9.80	0.41	0.0001
c	0.15–0.199	20.05	–17.50	602	16.10	0.44	0.0001
d	0.20–0.249	20.15	–19.22	220	11.64	0.48	0.0001
e	0.25–0.299	21.53	–19.13	214	12.32	0.48	0.0001
f	0.30–0.349	22.65	–20.69	260	11.05	0.58	0.0001
g	0.35–0.399	19.27	–15.87	221	10.70	0.34	0.0001
h	0.40–0.449	23.09	–20.44	181	5.13	0.61	0.0001
i	0.45–0.549	22.02	–16.14	124	13.43	0.37	0.0001
j	≥ = 0.55	23.40	–19.33	220	11.59	0.43	0.0001

data grouped by the growth parameter K (Fig. 5, A–J). With the exception of groupings for K<0.15 (Fig. 5, A and B), which have smaller intercept and slope values, the regressions are similar (Fig. 5, C–J). The regression line and the 95% confidence intervals are also shown and the associated statistics are given in Table 4. The slopes of the regressions are all significantly different from 0 (P<0.001).

Discussion

A number of LFA methods, especially those that estimate parameters by maximum likelihood methods, allow constraints on measures of dispersion. For example, the simplex method of Kumar and Adams (1977) incorporates linear constraints on the standard deviations (SD's) of normal components. The SD's can be equal or fixed and the coefficient of variation (CV) can be fixed or constant in the program MIX (Macdonald and Pitcher, 1979; Macdonald and Green, 1985). The SD's can be linear functions of mean length or of age in the Schnute and Fournier (1980) method. MULTIFAN (Otter Software, 1988) allows age-dependent or length-dependent trends in SD's. A common CV between 0.01 and 0.5 for all lengths at age or SD's that increase linearly with mean length was proposed for LFA constraints by Liu et al. (1989)

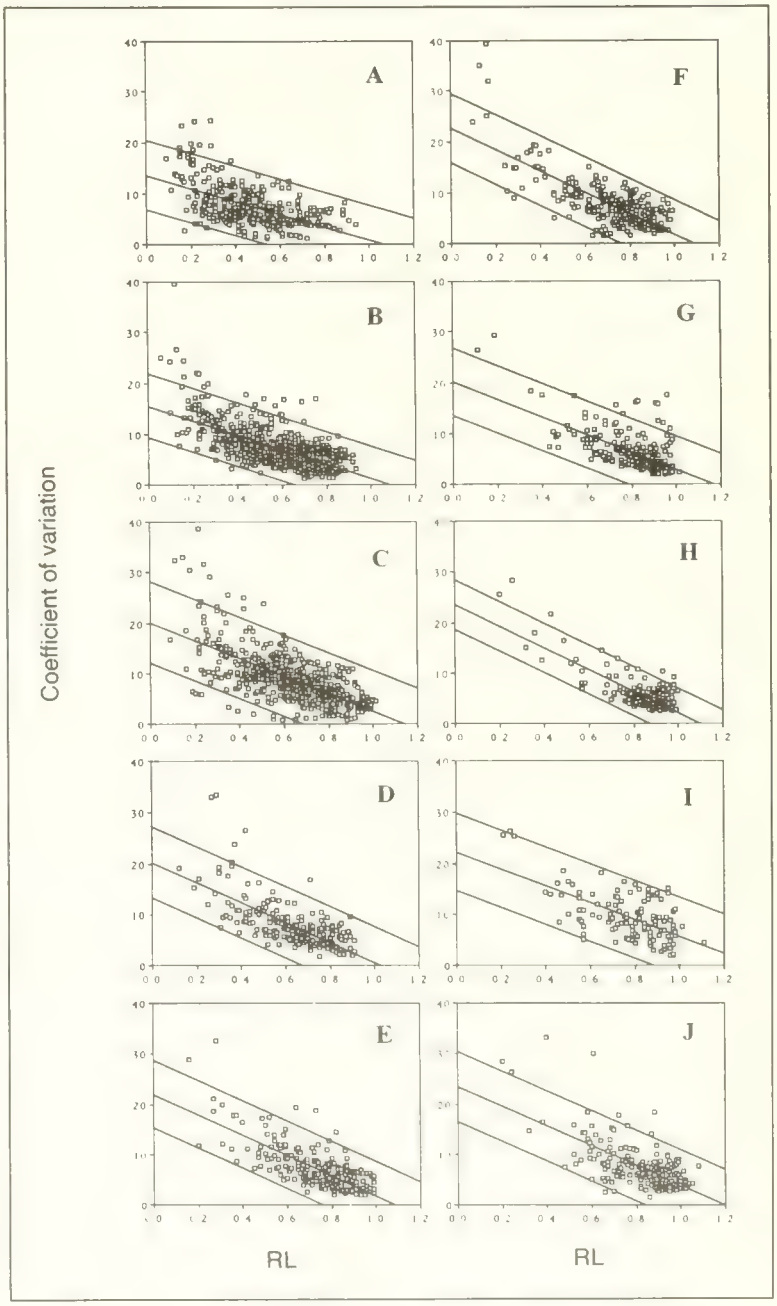

Figure 5

The coefficient of relative variation as a function of relative length for data grouped by K. RL is relative length (L_t/L_∞, length-at-age divided by L_∞). The interval classes and the regression statistics are given in table 4. Parallel lines are 95% confidence intervals.

In addition to these methods which allow specific constraints, some iterative methods require starting or initial values for some parameters, such as number of components, corresponding mean lengths at age, proportion in each age class and SD's of the component distributions (e.g. Akamine, 1982, 1984, 1985).

Our results can be used to select appropriate constraints and starting values for measures of dispersion for LFA methods. We have shown that the magnitudes of SD and V are dependent to a large extent on life history parameters. Therefore, if the LFA user has estimates of growth parameters, the multiple linear regression models in Table 1 can be used to estimate the SD for the species and size in question.

However, in most cases the objective of LFA is to estimate growth parameters, which are therefore not available for input into the predictive models. In this case, the CV may be more useful as a constraint. While the magnitudes of SD and V of mean length at age are related to characteristics of each species, relative variability in length at age (CV) is similar in species that differ greatly in life history parameters. Furthermore, while there are no consistent age- and size-dependent trends in absolute measures of variability, relative variability decreases in a predictable manner in almost all cases.

This was confirmed in a previous investigation of the shapes, magnitude, and age and size dependence of length-at-age distributions of marine fishes (Erzini, 1994). Analysis of 415 individual data sets showed that in 97% of the data sets the CV was negatively related to relative length at age, and the slope was significant ($P<0.05$) in 53% of the sets. CV values were similar for all species. A negative relationship between CV and size and decreasing variation with size are to be expected because changes in variability with growth are typically of smaller magnitude than changes in size with growth.

In contrast, although there was no dominant size-dependent or age-dependent trend for the SD, the most common pattern was that of increasing variability to a maximum at an intermediate age or size. This trend for increasing variability to a maximum at an intermediate size is illustrated in Figure 1, where the SD is plotted against relative length and asymptotic maximum length (L_∞). It is particularly evident for species with large L_∞ values.

In conclusion, we believe that the practical implications for LFA are that these empirically derived relationships between measures of dispersion, size, age, and life history parameters can be used to select starting values and to impose constraints on measures of dispersion corresponding to particular lengths at age. This is useful as there are no well established rules or guidelines for this process, which consequently has been highly subjective and dependent on each LFA user.

The choice of model depends on the availability of the data for the independent variables of the models. In the absence of any such data, the simplest model of the CV as a function of relative length can be used. As a preliminary step, length-frequency distributions should be examined and the number of possible component distributions and modes that may represent mean lengths at age identified visually. An estimate of L_∞ obtained from the literature or on the basis of the maximum observed size can be used to convert lengths to relative lengths. The estimated CV values and their corresponding confidence intervals for these modes can then be estimated with the models presented in this study. One possible approach is to use the estimated CV's as starting values and the confidence intervals as lower and upper constraints. Such a strategy would provide realistic starting values, reasonably narrow constraints, and would improve the often arbitrary choices which are made.

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Literature cited

Akamine, T.
1982. A BASIC program to analyze the polymodal frequency distributions into normal distributions. Bull. Jpn. Sea Fish. Res. Lab. 33:163–166.
1984. The BASIC program to analyze polymodal frequency distributions into normal distributions with Marquardt's method. Bull. Jpn. Sea Fish. Res. Lab. 34:53–60.
1985. Consideration of the BASIC programs to analyze the polymodal frequency distribution into normal distributions. Bull. Jpn. Sea Fish. Res. Lab. 35:129–160.

Basson, M, A. A. Rosenberg, and J. R. Beddington.
1988. The accuracy and reliability of two new methods for estimating growth parameters from length-frequency data. J. Cons. Int. Explor. Mer 44:277–285.

Castro, M., and K. Erzini.
1987. Comparison of two length frequency based methods used to obtain growth and mortality parameters using simulated samples with varying recruitment patterns. Fish. Bull. 86:645–653.

Erzini, K.
1990. Sample size and grouping of data for length frequency analysis. Fish. Res. 9:355–366.

1991. A compilation of data on variability in length-at-age of marine fishes. Fish. Stock Assess. CRSP Working Paper 77, 100 p.

1994. An empirical study of variability in length-at-age of marine fishes. J. Appl. Ichthyol. 10:17–41.

Gallucci, V. F., and T. J. Quinn.

1979. Reparametrizing, fitting, and testing a simple growth model. Trans. Am. Fish. Soc. 108:14–25.

Kumar, K. D., and S. M. Adams.

1977. Estimation of age structure of fish populations from length frequency data. *In* W. Van Winkle (ed.), Assessing the effects of power-plant induced mortality on fish populations, p. 256–281. Permagon Press, Oxford.

Liu, Q., T. Pitcher, and M. Al-Hossaini.

1989. Ageing with fisheries length-frequency data, using information about growth. J. Fish Biol. 35 (Suppl. A):169–177.

Longhurst, A. R., and D. Pauly.

1987. Ecology of tropical oceans. Academic Press, Inc.

Macdonald, P. D. M.

1987. Analysis of length frequency distributions. *In* R. C. Summerfelt (ed.), Age and growth of fish. Iowa State Univ. Press, p. 371–395.

Macdonald, P. D. M., and T. J. Pitcher.

1979. Age groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Board Canada 36:987–1001.

Macdonald, P. D. M., and P. E. J. Green.

1985. User's guide to program MIX: an interactive program for fitting mixtures of distributions. Ichthus Data Systems, 28 p.

Morgan, G.R.

1987. Incorporating age data into length-based stock assessment methods. *In* D. Pauly and G. R. Morgan (ed.), Length-based methods in fishery research: proceedings of the international conference on the theory and application of length-based methods for stock assessment; 11–16 February 1985, Mazzara del Vallo, Sicily, Italy. ICLARM Conf. Proc. 13:137–146.

Neter, J., W. Wasserman, and M. H. Kutner.

1983. Applied linear regression models. Richard D. Irwin, Inc., 547 p.

Otter Software.

1988. MULTIFAN, user's guide and reference manual. Nanaimo, B.C. Canada.

SAS Institute Inc.

1985. SAS® user's guide: statistics. SAS Institute Inc., 956 p.

Schnute, J., and D. Fournier.

1980. A new approach to length-frequency analysis: growth structure. Can. J. Fish. Aquat. Sci. 37:1337–1351.

Migratory characteristics of juvenile ocean-type chinook salmon, *Oncorhynchus tshawytscha*, in John Day Reservoir on the Columbia River

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Both stream-type and ocean-type chinook salmon, *Oncorhynchus tshawytscha*, are found in the Columbia River system. Ocean-type chinook salmon migrate seaward and enter seawater as subyearlings or zero-age juveniles within a year of emergence, whereas stream-type fish reside in fresh water at least one full year before migrating (Healey, 1991). Yearling stream-type chinook salmon migrate through the mainstem Columbia River and its largest tributary, the Snake River, during the spring months (Raymond, 1979). In contrast, zero-age ocean-type chinook salmon migrate during the summer, but their migration can extend into autumn. Information regarding the migratory behavior of ocean-type chinook salmon in the impounded reaches of the Columbia River is limited. Early research showed that even during high-flow years, large numbers of zero-age ocean-type chinook salmon remained in John Day Reservoir on the Columbia River for a protracted time compared with stream-type chinook salmon (Raymond et al.[1]; Sims et al.[2]).

Hydroelectric development has been identified as an important factor that has contributed to decreased salmon and steelhead (*Oncorhynchus* spp.) production in the Columbia River Basin (Raymond, 1979, 1988; Williams, 1989). Direct mortality of downstream migrant juvenile salmonids is associated with passage through the turbines, spillways, and juvenile bypass systems at dams. Apart from direct mortality, a number of studies have indicated that the creation of impoundments, altered flows resulting from electric power demand, and irrigation withdrawals as a result of dam construction have slowed the seaward migration of juvenile salmonids (Raymond, 1969, 1979; Ebel and Raymond, 1976).

In an effort to lessen deleterious effects associated with hydroelectric dam construction, fisheries managers have developed water management strategies to augment instream flows to provide improved passage conditions for juvenile salmonids during their seaward migration (Northwest Power Planning Council, 1987). Rationale supporting these actions is based largely on data by Sims and Ossiander[3] which described the migratory characteristics of juvenile stream-type chinook salmon and steelhead, *O. mykiss*, within the Snake River and in portions of the Columbia River. They found that increased instream flow volumes during the spring reduced smolt travel time through the hydroelectric complex and increased smolt survival. Similar data for ocean-type chinook salmon that migrate during the summer as zero-age juveniles are not available.

Berggren and Filardo (1993) suggested that increased water velocity increased migration speed for ocean-type chinook salmon and led to increased survival by reducing exposure time to predatory fish and to increasing summer water temperatures. There is ample evidence that predatory fish, principally northern squawfish, *Ptychocheilus oregonensis*, are abundant and consume large numbers of juvenile salmonids particularly during the summer in John Day Reservoir (Rieman et al., 1991; Vigg et al., 1991). However, the relationships between flows, migration rate, and survival are uncertain.

[1] Raymond, H. L., C. W. Sims, R. C. Johnsen, and W. W. Bentley. 1975. Effects of power peaking operations on juvenile salmon and steelhead trout migrations, 1974. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corps of Engineers, 46 p.

[2] Sims, C. W., R. C. Johnsen, and W. W. Bentley. 1976. Effects of power peaking operations on juvenile salmon and steelhead trout migrations, 1975. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corps of Engineers, 36 p.

[3] Sims, C. W., and F. J. Ossiander. 1981. Migrations of juvenile chinook salmon and steelhead trout in the Snake River from 1973 to 1979: a research summary. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corps of Engineers, 31 p.

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Developing water management strategies to benefit the juvenile stages of ocean-type chinook salmon has become an important issue in the Pacific Northwest; however, basic information describing migratory characteristics is required before such strategies can be designed. We undertook the present investigation to describe the migratory characteristics of ocean-type chinook salmon in John Day Reservoir, a major impoundment on the Columbia River. This paper describes the movement and residence time of zero-age ocean-type chinook salmon within the reservoir and examines the relationship between migration time through the reservoir and key environmental variables.

Study area

John Day Dam is a hydroelectric project on the Columbia River at river kilometer (rkm) 345, approximately 200 km east of Portland, Oregon (Fig. 1). The project was constructed and is operated by the U.S. Army Corps of Engineers (COE). The John Day Reservoir is the largest impoundment on the river, extending 122 km upstream to the tailrace of McNary Dam, located approximately 52 km downstream from the confluence of the Columbia and Snake rivers. The width of the reservoir ranges from 0.8 to 4.2 km, and its mid-pool depth extends to 48 m. The dam is approximately 1 km in length and is currently fitted with 16 turbines.

Methods

Migrant zero-age chinook salmon entering the juvenile fish sampling facilities at McNary Dam were collected from mid-June through August 1981 through 1983. The fish were predominantly a mixture of fall and summer races (named for the time of adult returns) from the Columbia River and some small portion of fall races from the Snake River. The yearling chinook migration peaks during May at McNary Dam but can extend from April into June (FPC[4]). By mid-June more than 95% of the yearlings have passed the dam. During late June some yearlings remain mixed with the zero-age migrants. To minimize the inclusion of the larger yearlings in our experimental groups we used fish less than 110-mm fork length during June. Each week, up to three groups of fish were freeze branded with a unique mark (Mighell, 1969). All fish bearing the same brand were released into the tailrace below McNary Dam at 2100 h on their respective release dates to continue their downstream migration.

[4] Fish Passage Center. 1992. Fish Passage Center 1991 Annual Report. Columbia Basin Fish and Wildlife Authority, Portland, OR, 52 p.

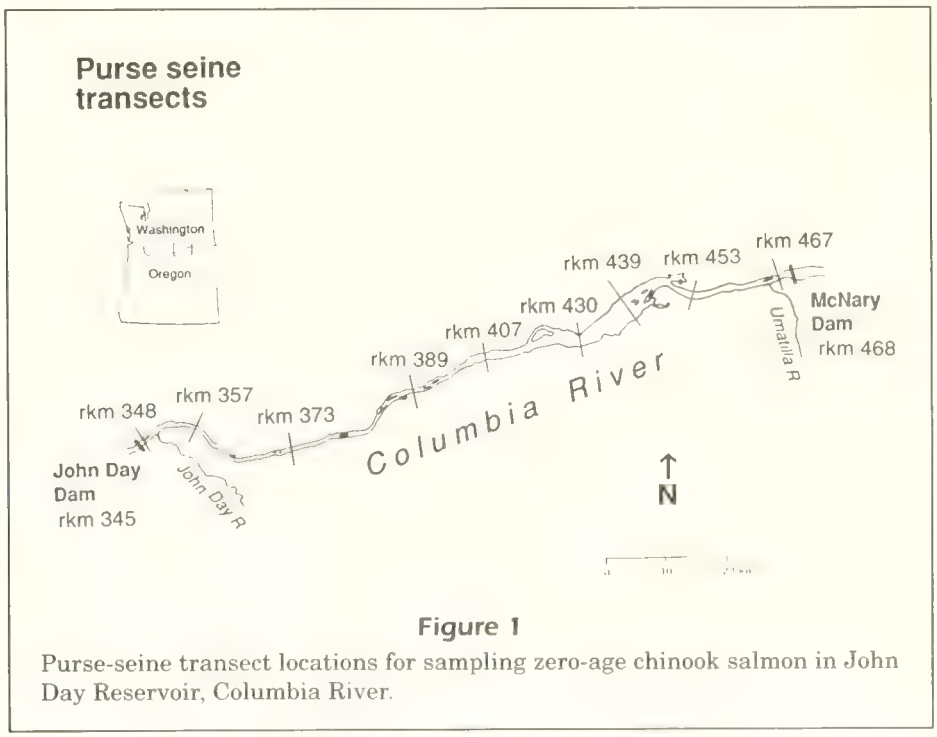

Figure 1

Purse-seine transect locations for sampling zero-age chinook salmon in John Day Reservoir, Columbia River.

Some of the freeze-branded fish were subsequently recovered downstream at John Day Dam. An airlift pump (Sims et al.[5]) was used to extract fish from the gatewells at Turbine Unit 3; however, it was unknown what proportion of recovered fish represented those passing into the turbine intake. Reliable estimates of that proportion are not available. Each day, collected fish were examined and brands enumerated. To provide a relative measure of daily passage at John Day Dam, the daily catch was expanded in proportion to the daily total river flow that was discharged through the sampled turbine unit. That proportion varied with prevailing spill volumes and the number of turbine units that were operating. Some water was also discharged through the navigation locks and fish ladders, but the amount was small, typically less than 1% of the total river discharge (Sims et al.[6]). The expanded daily catch was referred to as the passage index and was a relative measure of the number of fish passing the entire dam. The calculation of the passage index assumed 1) that the proportion of fish passing the dam through the spillway was equal to the proportion of water spilled, and 2) that the proportion of fish entering the gatewells from the turbine intake was relatively constant.

For each branded group, we constructed a distribution of daily passage indices. The median migration time for each group was estimated as the elapsed time between the known release date at McNary Dam and the date of median passage index distribution at John Day Dam. In addition, we estimated the passage index for the entire population passing John Day Dam each week.

Additionally, to characterize the movement patterns within John Day Reservoir, we freeze-branded, released, and subsequently recaptured zero-age chinook salmon at fixed cross-sectional transects located along the length of the reservoir (Fig. 1). We sampled fish with a 305 × 11 m purse seine (12-mm stretched mesh, knotless web throughout) aboard an 11-m power-block seiner. At each transect, a seine set was made as close to each shore as possible, allowing a minimum depth of 5 m for the seiner; the skiff would extend the net toward shore. A third set was executed at midreservoir. Sampling continued throughout the summer and autumn until late November each year. Sampling extended from the forebay at John Day Dam (rkm 348) to the McNary Dam tailrace (rkm 467). We initially established and sampled nine transects spanning the length of the reservoir (Fig. 1). However, catches were so small at the three locations farthest upstream that we discontinued sampling those sites halfway through the 1981 sampling period. We cycled through all transects approximately every other week. All fish were anesthetized with MS-222, counted, and examined for marks. Unmarked fish were freeze branded, a subsample was measured for fork length, and after processing, all fish were allowed to recover from the anesthetic and were released.

To examine the effects of several key variables on migration rate from McNary to John Day Dam, we used correlation and regression techniques, analyzing each year separately and pooled together. The dependent variable was the median migration time (travel time) for each release group. The independent variables included release date, water temperature, and inverse river-flow volume. We used the inverse of volume, based on the hypothesis that fish would most likely respond to water velocity (water velocity is the river-flow volume divided by the cross-sectional area) and that fish travel time is related to water particle travel time, which is functionally inversely related to water velocity. Water temperature and flow were represented by a daily average over the 10-day period following the release date of each marked group. Water temperature and flow data were acquired from the COE. All data were originally reported by Giorgi et al.[7]

Results

Migration timing and migrant size

Each year, there was a minor peak in abundance of zero-age chinook salmon passing McNary Dam near the beginning of July and a major peak at the end of July (Fig. 2). In 1982 and 1983, the migration times for the zero-age chinook salmon populations passing John Day Dam were nearly identical. In 1982, 90% of the outmigrants had passed John Day Dam by the week ending 4 September and in 1983, by 26 August. In 1981, the passage distribution was somewhat dissimilar to those of 1982 and 1983; however, the 90th percentile of passage occurred during the week end-

[5] Sims, C. W., J. G. Williams, D. A. Faurot, R. C. Johnsen, and D A. Brege. 1981. Migrational characteristics of juvenile salmon and steelhead in the Columbia River Basin and related passage research at John Day Dam, Vols. I and II. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corps of Engineers, 61 p.

[6] Sims, C. W., A. E. Giorgi, R. C. Johnsen, and D. A. Brege. 1983. Migrational characteristics of juvenile salmon and steelhead in the Columbia River Basin — 1982. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corp of Engineers, 35 p.

[7] Giorgi, A. E., D. R. Miller, and B. P. Sandford. 1990. Migratory behavior and adult contribution of summer outmigrating subyearling chinook salmon in John Day Reservoir. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to Bonneville Power Administration, 68 p.

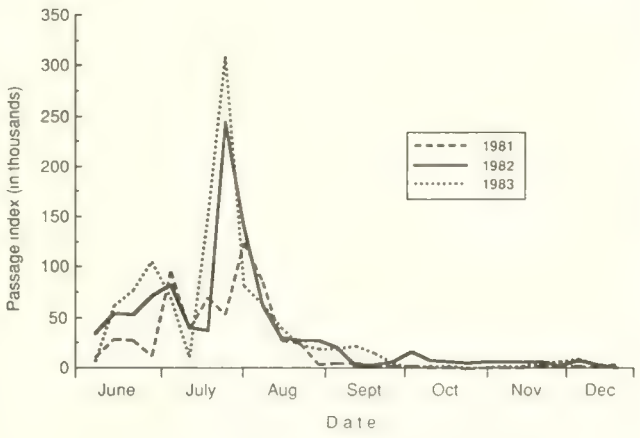

Figure 2

Weekly passage indices of zero-age chinook salmon passing John Day Dam, Columbia River. The dashed, solid, and dotted lines represent 1981, 1982, and 1983, respectively.

ing 22 August, the same general time frame as in the following years.

Migrant size increased steadily over the course of the sampling period in all years. The mean size ranged from approximately 90 mm in early June to near 145 mm by the end of August. By mid-December, the length of fish passing John Day Dam averaged approximately 170 mm. The smallest migrants observed passing either McNary or John Day Dam were 55 to 60 mm during the month of June each year. The largest migrants approached 225 mm in December. The fish sampled at all three sites (McNary Dam, John Day Dam, and within the reservoir) displayed the same size distributions during the sampling periods.

Environmental conditions

Each year the trend in river flow was similar: discharge consistently decreased during the summer. However, the absolute flow volumes varied considerably over the three years of study (Tables 1–3). The greatest differences in flow volumes were observed each year from mid-June to mid-July. Beyond that period, flow volumes were nearly the same from year to year. The highest flow year occurred in 1982 when discharge levels averaged up to 11.11×10^3 cubic meters per second during the last week of June. Overall, the lowest flows occurred in 1983. For example, during the last week of June, river discharge volumes were nearly half the maximum level observed in 1982, averaging between 5.91×10^3 and 6.87×10^3 cubic meters per second.

Water temperatures were similar among years and displayed the same tendency to increase throughout the summer (Tables 1–3). Early in the summer, water

Table 1

Summary of 1981 brand release and recovery data from groups of zero-age chinook salmon marked and released at McNary Dam and recaptured at John Day Dam. Travel time is the number of days required to traverse the reservoir from McNary Dam tailrace to John Day Dam. The percentiles were calculated from the passage indices.

Release date	Number of fish			Flow[2] $m^3 \cdot sec^{-1}$ $(\times 10^3)$	Temperature[2] (°C)	Travel time (days)		
	Released	Recovered	Passage index[1]			Percentiles 10	50	90
6/15	3,325	28	437	9.76	15	16	18	23
6/18	4,654	44	667	9.25	15	14	16	26
6/24	3,458	37	554	7.49	16	2	10	26
6/29	6,286	38	591	7.16	16	5	7	17
7/10	10,115	79	840	6.36	16	10	19	33
7/16	10,143	65	628	5.94	17	13	21	37
7/22	10,012	50	526	5.66	18	5	14	22
7/29	12,310	64	624	5.43	19	7	9	50
8/03	2,512	11	105	5.06	19	5	6	18
8/10	2,663	15	113	4.66	19	11	17	98
8/13	2,545	12	81	4.33	20	8	26	126
8/17	2,547	10	63	4.13	21	4	18	24
8/20	2,536	22	145	3.87	21	7	19	81
8/26	1,577	6	35	3.56	21	5	13	33

[1] The passage index is calculated daily as the ratio of the number recovered to the sampling effort and summed over days. Sampling effort was the average proportion of the total river flow discharged through Turbine Unit 3 during the 10-hour period 2000–0600 h.
[2] The average river-flow volume and water temperature over the 10-day period following release of the marked group.

Table 2

Summary of 1982 brand release and recovery data from groups of zero-age chinook salmon marked and released at McNary Dam and recaptured at John Day Dam. Travel time is the number of days required to traverse the reservoir from McNary Dam tailrace to John Day Dam. The percentiles were calculated from the passage indices.

	Number of fish					Travel time (days)		
				Flow[2]		Percentiles		
Release date	Released	Recovered	Passage index[1]	$m^3 \cdot sec^{-1}$ ($\times 10^3$)	Temperature[2] (°C)	10	50	90
6/24	2,396	7	148	11.11	16	6	9	46
6/26	3,235	17	346	10.92	16	5	13	27
6/29	2,690	9	136	10.44	16	12	22	92
7/13	3,035	15	181	6.96	18	3	16	87
7/15	4,323	13	143	6.42	18	7	18	78
7/17	4,012	17	219	6.82	18	6	13	25
7/20	5,001	16	172	5.80	19	7	17	71
7/22	2,012	19	168	5.54	18	14	31	78
7/27	3,262	33	299	5.46	20	8	19	59
7/29	4,500	44	368	5.43	20	8	24	71
8/03	1,007	7	63	5.37	20	5	34	90
8/05	2,383	29	253	5.10	20	7	24	78
8/10	3,000	32	259	4.52	20	5	12	76
8/13	2,571	31	247	4.16	20	9	46	68
8/17	3,450	46	321	4.02	20	12	41	76
8/20	3,005	31	231	3.39	21	7	39	62
8/24	1,467	22	160	3.34	21	6	35	59
8/27	3,581	35	246	3.17	21	12	31	46
8/31	1,589	16	133	3.70	21	9	23	59
9/03	4,541	16	125	3.79	20	9	45	98

[1] The passage index is calculated daily as the ratio of the number recovered to the sampling effort and summed over days. Sampling effort was the average proportion of the total river flow discharged through Turbine Unit 3 during the 10-hour period 2000–0600 h.
[2] The average river-flow volume and water temperature over the 10-day period following release of the marked group.

Table 3

Summary of 1983 brand release and recovery data from groups of zero-age chinook salmon marked and released at McNary Dam and recaptured at John Day Dam. Travel time is the number of days required to traverse the reservoir from McNary Dam tailrace to John Day Dam. The percentiles were calculated from the passage indices.

	Number of fish					Travel time (days)		
				Flow[2]		Percentiles		
Release date	Released	Recovered	Passage index[1]	$m^3 \cdot sec^{-1}$ ($\times 10^3$)	Temperature[2] (°C)	10	50	90
6/16	4,839	41	601	6.87	13	5	11	30
6/23	5,196	23	327	5.91	14	15	19	26
7/01	5,010	28	421	5.54	16	8	15	19
7/08	4,988	35	557	5.60	16	9	12	24
7/13	5,005	20	333	6.14	16	3	7	23
7/15	5,014	42	627	5.97	16	4	7	24
7/20	5,019	60	700	6.00	17	7	19	53
7/23	5,009	62	596	5.80	18	7	29	50
7/27	4,659	41	374	5.71	18	12	25	98
7/29	5,939	71	621	5.46	18	9	29	83
8/05	4,657	60	499	4.84	19	6	24	115
8/12	4,850	39	304	4.67	20	6	28	101
8/19	4,878	47	363	4.10	21	4	23	73
8/26	5,641	54	417	3.59	19	5	15	84
9/02	1,855	17	127	3.40	18	6	9	59

[1] The passage index is calculated daily as the ratio of the number recovered to the sampling effort and summed over days. Sampling effort was the average proportion of the total river flow discharged through Turbine Unit 3 during the 10-hour period 2000–0600 h.
[2] The average river-flow volume and water temperature over the 10-day period following release of the marked group.

temperatures ranged from 13 to 16°C, then increased steadily during the summer and peaked near 21°C by the end of August. Overall, 1982 was characterized by slightly higher water temperatures than the other two years.

Fish travel time from McNary Dam to John Day Dam

For the three study years, a total of 49 freeze-branded groups were released to estimate fish travel time through the reservoir. The number of fish released in each group ranged from 1,007 to 12,310 (Tables 1–3). The estimated median travel time through John Day Reservoir for freeze-branded groups ranged from 6 to 26 days in 1981, 9 to 46 days in 1982, and 7 to 29 days in 1983 (Tables 1–3). Overall, the estimated median travel times were longest in 1982.

All individual groups exhibited protracted passage distributions at John Day Dam. The elapsed time between the 10th and 90th percentile of the recapture distributions typically exceeded several weeks (Tables 1–3). The fastest moving fish, those represented by the 10th percentile, traversed the reservoir in 2 to 16 days. The slowest moving fish, those represented by the 90th percentile, took 17 to 126 days to migrate through the reservoir.

The linear regression analyses, treating each year separately and pooling all years, did not identify a single model that was applicable to all years. Transformation of predictor variables did not improve the model. In fact, for each year, different sets of variables were included in the model constructed by the stepwise procedure. In 1981, the variability in travel time could not be explained by any predictor (Table 4), and none of the predictor variables entered the model. In 1982, only one predictor, release date, was entered into the model. In 1983, two variables, release date and water temperature, were entered into the model. For the three years combined, only water temperature entered into the model. In all years, strong correlations were observed among the three predictor variables, with r-values ranging from 0.64 to 0.98.

Table 4

Regression models derived from stepwise multiple regression. The modelling procedure was applied to median zero-age chinook salmon travel times presented in Tables 1–3. Average water temperature, inverse average flow, and Julian release date were used in the model selection process.

Year	Model	R^2
1981	No variables were entered into the model	0.00
1982	Travel time = –53.02 + 0.37 (release date)	0.47
1983	Travel time = –1.16 + 5.20 (temperature) –0.34 (release date)	0.46
Combined	Travel time = –22.83 + 2.36 (temperature)	0.24

Intrareservoir movement

Upstream movement of fish after branding was regularly observed in the reservoir (Table 5). Detailed recapture histories for individual fish were reported in Sims and Miller,[8] and Miller and Sims.[9,10] In 1981, 1982, and 1983, the percentages of marked fish that were recaptured at or upstream from the transect of release were 67, 63, and 60%, respectively (Table 5). In each year, upstream movement was observed more frequently than stationary or downstream movement. Upstream movements were often pronounced, ranging from 9 to 82 km. Over the three years of study, the duration of the observed upstream movements ranged from 6 to 104 days. These observations indicated that the population at large was not consistently displaced downstream: rather, a large segment was engaged in pronounced upstream movement, or was stationary for extended periods.

[8] Sims, C. W., and D. R. Miller. 1982. Effects of flow on the migratory behavior and survival of juvenile fall and summer chinook salmon in John Day Reservoir. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to Bonneville Power Administration, 22 p.

[9] Miller, D. R., and C. W. Sims. 1983. Effects of flow on the migratory behavior and survival of juvenile fall and summer chinook salmon in John Day Reservoir. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to Bonneville Power Administration, 25 p.

[10] Miller, D. R., and C. W. Sims. 1984. Effects of flow on the migratory behavior and survival of juvenile fall and summer chinook salmon in John Day Reservoir. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to Bonneville Power Administration, 23 p.

Table 5

Purse-seine recoveries of marked zero-age chinook salmon that were previously marked and released at various John Day Reservoir sampling transects, 1981–83.

	1981	1982	1983
Number of release groups	34	44	32
Number of fish released	14,273	13,126	22,206
Number of fish recaptured at transects in reservoir	63	41	111
Proportion recaptured at			
release site	0.11	0.12	0.16
upstream transects	0.56	0.51	0.44
downstream transects	0.33	0.37	0.40
Upstream recaptures			
excursion length; range (km)	10–80	16–82	9–82
excursion duration; range (d)	6–75	8–104	6–79

Discussion

Our analyses indicated that no consistent set of predictors (water temperature, release date, or flow) could explain the travel time of zero-age ocean-type chinook salmon through John Day Reservoir. The predictors for travel time changed each year. The stepwise regression procedure failed to find any statistically significant variables to explain results in 1981, and flow was not a statistically significant predictor in any year. However, strong correlations among all predictor variables suggested that flow was nearly equally as likely a predictor as water temperature in 1983 and in the combined years, or as release date in 1982 and 1983.

Release date was included as a predictor variable to provide a generic measure to characterize time-based changes in fish development, such as size or physiological changes that progress over the course of the migration period. Since release date entered the model in two of the three years, this suggested that some time-based biological process may have been important. However, the strong correlations among predictor variables in each year limited the utility of such multivariable regression analyses for identifying the importance of any particular variable. Furthermore, in examining bivariate correlations we found no consistent relationships between migration time and any predictor variable.

Other measures of migratory behavior should be considered when characterizing the migratory dynamics of a population. One such measure we considered involved describing the directional intrareservoir movement of fish. We observed that within the body of the reservoir, zero-age ocean-type chinook salmon did not exhibit consistent downstream movement indicative of a continual, directed seaward migration. The majority of fish that were marked and released at transects throughout the reservoir were recaptured at or upstream from the site of release. This indicated that the population was not consistently displaced downstream passively via current. Based on laboratory observations of coho salmon, *O. kisutch*, Smith (1982) suggested that smolts in the Columbia River may be oriented mostly head-first upstream during outmigration, thus drifting downstream tail-first while being swept seaward. Our results indicate that zero-age chinook salmon do not fit this conceptual model.

The protracted reservoir-residence times apparent in our data are not necessarily peculiar to Columbia River stocks. Reimers (1973) studied fall chinook salmon in the Sixes River, Oregon, and suggested the optimum size at ocean entry is about 130 mm for that stock. He noted that this length was attained by juveniles that remained in fresh or estuarine waters for extended periods of time, suggesting that extended freshwater residence is beneficial to zero-age fall chinook salmon. Extended residence of zero-age chinook salmon was observed in the Columbia River during the late 1950's (Mains and Smith, 1964), and even prior to dam construction (Rich, 1922).

The absence of a strong relationship between the migration rate and water velocity (flow) for ocean-type chinook salmon contrasts with evidence linking travel time to flow (Sims and Ossiander[3]; Sims et al.[6]), or developmental (smoltification) state, or both (Giorgi, 1990; Berggren and Filardo, 1993; Beeman et al.[11]) for migratory yearling stream-type chinook salmon.

The effects of smolt development on migratory behavior of zero-age fish are not clear. Zaugg (1982) cited a number of examples that suggested smolt development might be an important process governing migratory behavior of zero-age fall chinook salmon. In contrast, investigations conducted in the Rogue River, Oregon, indicated smolt development was not a requirement for downstream migration in ocean-type juveniles and its importance in affecting the rate of migration was not apparent (Ewing et al., 1980). Although the regression analysis in our investigation used a surrogate variable that may reflect smoltification-related effects (release date), its adequacy in representing such effects has not been verified. Future investigations should include direct assessments of effects associated with developmental processes, such as sodium and potassium ion levels and gill ATPase levels, as well as migrant size.

Berggren and Filardo (1993) also examined the relationship between travel time and a host of predictor variables for zero-age chinook salmon in John Day Reservoir. Their analysis included a subset of our data, as well as similar releases that were executed in 1986–88 (Harmon et al.[12]). In their multivariable approach, data were pooled across years. The variables in the final multiple regression model included release date, inverse flow, and an index of the absolute change in flow. The bivariate relationship between smolt travel time and inverse flow had an associated r^2 value of 0.28. In contrast to our results, they concluded that increased flows reduced travel time of zero-age chinook salmon.

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[11] Beeman, J. W., D. Rondorf, J. Faler, M. Free, and P. Haner. 1990. Assessment of smolt condition for travel time analysis. U.S. Fish Wild. Serv., Cook, WA 98605. Report to Bonneville Power Administration, 71 p.

[12] Harmon, J. R., G. M. Matthews, D. L. Park, and T. E. Ruehle. 1989. Evaluation of transportation of juvenile salmonids and related research on the Columbia and Snake Rivers, 1988. Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097. Report to U.S. Army Corp of Engineers, 11 p.

The variability in travel-time estimates observed in this study may in part have resulted from limited sampling capability at John Day Dam, since only 0.3 to 1.3% of any marked group was recovered at that site. There were four groups from which less than 10 recaptures were observed (Tables 1 and 2). However, the travel-time estimates of Berggren and Filardo (1993) displayed generally the same range of values, even though sampling effort at John Day Dam was increased during the latter years on which their analyses were based.

Another confounding factor is that our investigation treated the entire composite population of zero-age juveniles. For future studies, we suggest studying individual stocks of fish to describe any unique migratory characteristics that may be stock-specific.

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Literature cited

Berggren, T. J., and M. J. Filardo.
1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River Basin. N. Am. J. Fish. Manage. 13(1):48–63.

Ebel, W. J., and H. L. Raymond.
1976. Effects of atmospheric gas saturation on salmon and steelhead trout of the Snake and Columbia rivers. Mar. Fish. Rev. 38(7):1–14.

Ewing, R. D., C. A. Fustish, S. L. Johnson, and H. J. Pribble.
1980. Seaward migration of juvenile chinook salmon without elevated gill (Na + K)-ATPase activities. Trans. Am. Fish. Soc. 109:349–356.

Giorgi, A. E.
1990. Biological manipulation of migratory behavior: the use of advanced photoperiod to accelerate smoltification in yearling chinook salmon. *In* D. L. Park (convener), Status and future of spring chinook salmon in the Columbia River Basin—conservation and enhancement; proceedings of the spring chinook workshop, 8–9 November 1989, p. 108–114. NOAA Tech. Memo. NMFS F/NWC-187, Northwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA 98112-2097.

Healey, M. C.
1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). *In* C. Groot, and L. Margolis (eds.), Pacific salmon life histories. UBC Press, Vancouver, Canada, 564 p.

Mains, E., and J. Smith.
1964. The distribution, size, time and current preferences of seaward migrant chinook salmon in the Columbia and Snake Rivers. Wash. Dep. Fish., Fish. Res. Pap. 2(3):5–43.

Mighell, J. L.
1969. Rapid cold-branding of salmon and trout with liquid nitrogen. J. Fish. Res. Board Can. 26:2765–2769.

Northwest Power Planning Council.
1987. Columbia Basin fish and wildlife program. Northwest Power Planning Council, Portland, OR 97204, 246 p.

Raymond, H. L.
1969. Effect of John Day Reservoir on the migration rate of juvenile chinook salmon in the Columbia River. Trans. Am. Fish. Soc. 98(3):513–514.
1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. Trans. Am. Fish. Soc. 108:529–565.
1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River Basin. N. Am. J. Fish. Manage. 8(1):1–24.

Reimers, P. E.
1973. The length of residence of fall chinook salmon in Sixes River. Oreg. Fish Comm. Res. Rep. 4:2–43.

Rich, W.
1922. Early history and seaward migration of chinook salmon in the Columbia and Sacramento Rivers. U.S. Bur. Fish., Bull. 37:1–74.

Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe.
1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. Trans. Am. Fish. Soc. 120:448–458.

Smith, L. S.
1982. Decreased swimming performance a necessary component of the smolt migration in salmon in the Columbia River. Aquaculture 28:153–161.

Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel.
1991. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. Trans. Am. Fish. Soc. 120:421–438.

Williams, J. G.
1989. Snake River spring and summer chinook salmon: Can they be saved? Regul. Rivers Res. & Manage. 4:17–26.

Zaugg, W. S.
1982. Relationships between smolt indices and migration in controlled and natural environments. *In* E. L. Brannon and E. O. Salo (eds.), Proceedings of the salmon and trout migratory behavior symposium, Seattle, 1981. School of Fish., Univ. Wash., Seattle, WA 98195, p. 173–183.

Comparisons between generalized growth curves for two estuarine populations of the eel tailed catfish *Cnidoglanis macrocephalus*

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The eel tailed catfishes (Plotosidae) are distributed throughout the Indo-west Pacific region and comprise approximately 30 species. Just over half of these species are found in Australian waters (Hoese and Hanley, 1989). The estuarine catfish or cobbler, *Cnidoglanis macrocephalus* Günther, is one of three plotosid species that are found in the marine and estuarine waters of the southwestern region of Australia (Kowarsky, 1976; Hutchins and Swainston, 1986). *Cnidoglanis macrocephalus* can complete its life cycle in estuaries as well as in coastal marine waters (Laurenson et al., 1993a), suggesting that the populations of this species in each of the different estuaries represent separate demes, a view supported by the results of electrophoretic studies (Ayvazian et al., 1994).

Cnidoglanis macrocephalus is the most valuable of several teleosts fished commercially in Western Australian estuaries (Lenanton and Potter, 1987). While the permanently open Swan and Peel-Harvey estuaries on the southwestern coast of Western Australia were previously the main contributors to the fishery for this species (Laurenson et al., 1992), this role has now been assumed by Wilson Inlet on the southern coast of the state (Laurenson, 1992; Laurenson et al., 1993b). In contrast to the Swan and Peel-Harvey estuaries, Wilson Inlet is seasonally closed and, because of its more southerly location, does not reach as high a temperature in the summer (c.f. Loneragan et al., 1989; Potter et al., 1993).

Fish are commonly aged by counting the number of annuli on hard structures, such as scales, otoliths, vertebrae, or spines (e.g. Beamish and McFarlane, 1983; Casselman, 1987). However, prior to carrying out such counts, it is important to validate that each of the sequential growth zones is formed annually (e.g. Beamish and McFarlane, 1983; Beckman et al., 1989; Collins et al., 1989; Hyndes et al., 1992). Although Nel et al. (1985) showed that the translucent zones in the asterisci of *C. macrocephalus* from the Swan Estuary tended to be formed annually, their results were based on pooled data for all fish and, thus, did not verify that this applied equally to each of the sequential translucent zones. Moreover, since the data for males and females were pooled, it was not possible to determine whether the growth rates of the two sexes in this system were the same.

A variety of different forms of growth equations can be calculated from 1) the lengths at given ages and 2) back calculations of body length at each annulus, using the relationship between body length and otolith radius. Both calculations use a predetermined "birth date" for the species. The effectiveness of using length-at-age data relies on obtaining representative samples of all age classes. Back calculations are particularly useful when certain age classes have not been sampled effectively but may produce biased estimates of the lengths of younger fish, i.e. Lee's phenomenon (Ricker, 1975). Furthermore, the lack of independence of the multiple measures for lengths at annulus formation obtained for a single fish by this method may introduce a statistical bias.

The aims of our study were 1) to validate that each of the sequential translucent growth zones on otoliths of *C. macrocephalus* in Wilson Inlet and the Swan Estuary correspond to an annulus and 2) to construct growth curves for each sex in both populations, using both lengths of fish at age of capture and back-calculated lengths. These curves were then used to compare a) growth between sexes within each estuary, b) growth between estuaries, and c) growth calculated using lengths at age and back-calculated lengths.

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Materials and methods

Collection of fish

Juvenile and adult *Cnidoglanis macrocephalus* were collected by seining at eight sites, gillnetting at nine sites, and otter trawling at six sites located throughout the basin of Wilson Inlet between September 1987 and April 1989 (see Fig. 1 in Potter et al. [1993] for location of this estuary and the sampling sites). Some of the sampling by each method was carried out monthly, while the rest was undertaken bimonthly (see Potter et al., 1993). The seine was 41.5 m long (stretched mesh = 51 mm in wings and 9.5 mm in pocket), while the gill net consisted of six 30-m contiguous panels, each with a different stretched mesh size, i.e. 38, 51, 63, 76, 89, or 102 mm. The stretched mesh in the wings and codend of the otter trawl were 51 and 25 mm, respectively. Seine netting and otter trawling were carried out during the day, while gillnetting was undertaken overnight. A small number of larval and post-larval *C. macrocephalus* were also collected in night-time plankton tows (Neira and Potter, 1992) and from their nests by dip net (Laurenson et al., 1993a).

Sampling in the Swan Estuary employed winged funnel traps between August 1982 and April 1983 (see Nel et al., 1985). Fish were also taken in a seine and otter trawl similar to those used in Wilson Inlet and with gill nets containing panels with the same mesh sizes as those employed in Wilson Inlet, but with additional panels of 13- and 25-mm mesh.

Validation of translucent zones as annuli and otolith measurements

The first 10 males and 10 females of *C. macrocephalus* caught in each panel of the gill nets at each site in Wilson Inlet on each sampling occasion, together with all fish caught in seine nets, were kept for ageing. All fish caught in otter trawls, except for a small number that were retained for tagging experiments, were also used for ageing. The total length and wet weight of each fish were recorded to the nearest 1 mm and 0.1 g, respectively. Each *C. macrocephalus* was sexed, except in the case of smaller fish (<ca. 100 mm) where the gonad could not be distinguished as either ovary or testis. The small, round asterisci and the larger, elongate lapilli otoliths were removed from fish and stored dry in envelopes.

Because preliminary examination showed that translucent zones were more clearly detectable in the lapilli than asterisci of *C. macrocephalus* from Wilson Inlet, lapilli were used for ageing this species in Wilson Inlet. The lapilli were placed in a bath of methyl salicylate and viewed under reflected light against a dark background with a dissecting microscope. The number of translucent zones on each otolith was recorded. Because the outermost opaque region of the otolith was not sharply defined, it was difficult to obtain consistent measurements of the distance between the outer translucent zone and the edge of the otolith. The mean monthly trends shown by the width of this marginal increment did not follow a very consistent pattern and therefore could not be used to establish that the outer zones on these otoliths were formed annually (see Maceina et al., 1987; Hyndes et al., 1992). To provide an alternative method for validating that each of the translucent zones corresponded to an annulus, the percentage of lapilli with a clearly defined translucent zone at the periphery of the otolith in each month was calculated separately for otoliths with one, two, three, four, and five or more inner translucent zones (e.g. Crozier, 1989; Beckman et al., 1990).

The difficulty in obtaining consistent measurements of the marginal increments in the lapilli of *C. macrocephalus* from Wilson Inlet was not encountered with the asterisci of this species from the Swan Estuary (Nel et al., 1985). The measurements of asterisci and total lengths of *C. macrocephalus* from the Swan Estuary were obtained from the raw data used by Nel et al. (1985). When two or more translucent zones were present, the relative values for the marginal increment were obtained by expressing the distance between the outer edge of the outermost translucent zone and the edge of the otolith as a percentage of the distance between the outer edges of the two outermost translucent zones. When only one translucent zone was present, the relative values were expressed as a percentage of the distance between the outer edge of the outermost translucent zone and the nucleus. The mean relative marginal increments are subsequently referred to as mean marginal increments. The distances between the nucleus of the otolith and the outer edge of each translucent zone and the outer edge of the otolith were measured to the nearest 0.05 mm along the long axis of lapilli and asterisci otoliths from Wilson Inlet and Swan Estuary, respectively.

Calculation of growth curves

The relationships $g(x)$ between the natural logarithms of total length (y) and lapillus radius (x) of *C. macrocephalus* in Wilson Inlet, and between the natural logarithms of total length and asteriscus radius of this species in the Swan Estuary, were described by a third order polynomial of the form $y = a + bx + cx^2 + dx^3$, where a, b, c, and d are constants. Back calculations of fish length at the formation of

each annulus followed a body proportional hypothesis (Francis, 1990), using the equation $L_i = L \exp[g(\ln(S_i)) - g(\ln(S))]$, where L_i is the estimated total length at the formation of the ith annulus, L is the total length at capture, S_i is the radius of the ith annulus, and S is otolith radius.

Lengths at age and back-calculated lengths were used to construct growth curves using the traditional form of the von Bertalanffy equation, $L_t = L_\infty(1 - \exp[-k(t - t_0)])$, where L_t is the mean body length of fish of age t, L_∞ is the asymptotic mean length of fish in the population, t_0 is the theoretical age at which the length of fish is zero, and k is the growth coefficient. Since the von Bertalanffy curves failed to describe adequately the full range of data (see Discussion), the more flexible growth curve equation derived by Schnute (1981) was fitted to the data. There are four possible forms of this equation, depending on the values of the parameters a and b, where y_1 and y_2 are the lengths of the fish at the specified ages T_1 and T_2 (i.e. ages 1 and 4, which bounded the majority of the data set in this application).

$$\text{Case 1:}\quad a \neq 0, b \neq 0 \qquad L_t = \left[y_1^b + (y_2^b - y_1^b)\frac{1-\exp(-a(t-T_1))}{1-\exp(-a(T_2-T_1))} \right]^{1/b};$$

$$\text{Case 2:}\quad a \neq 0, b = 0 \qquad L_t = y_1 \exp\left[\log\left(\frac{y_2}{y_1}\right)\frac{1-\exp(-a(t-T_1))}{1-\exp(-a(T_2-T_1))} \right];$$

$$\text{Case 3:}\quad a = 0, b \neq 0 \qquad L_t = \left[y_1^b + (y_2^b - y_1^b)\frac{t-T_1}{T_2-T_1} \right]^{1/b};$$

$$\text{Case 4:}\quad a = 0, b = 0 \qquad L_t = y_1 \exp\left[\log\left(\frac{y_2}{y_1}\right)\frac{t-T_1}{T_2-T_1} \right].$$

When $a > 0$ and $b = 1$, the generalized growth curve is equivalent to the traditional form of the von Bertalanffy growth curve, with $a = k$. The resultant form of the generalized growth equation was determined by the parameters a and b that resulted in the minimum sum of squared deviations. Data were fitted by using a nonlinear least squares method, employing the nonlinear (NLIN) procedure of SAS (Ihnen and Goodnight, 1987). All back calculations and curve fittings were carried out separately for each sex in both populations. Juveniles, for which the sex could not be determined, were included in calculating growth curves of both sexes from length-at-age data. Calculations of all curves assumed a birth date of 1 December in Wilson Inlet and 1 November in Swan Estuary (Laurenson et al., 1993a).

Each growth curve, fitted by using the traditional form of the von Bertalanffy growth equation, was compared with the corresponding generalized growth curve by using a likelihood ratio test, an approach adopted with several other fish species (Kimura, 1980; Kirkwood, 1983; Cerrato, 1990; Hampton, 1991; Buxton, 1993). The generalized growth curves of both sexes in Wilson Inlet and Swan Estuary based on lengths at age and back calculated lengths, were compared by using the same likelihood ratio test, which involved determining the improvement of fit obtained by using the two separate curves, rather than a common curve. This involved 1) comparing the curve for males with that for females in each system, using first lengths at age and then back-calculated lengths; 2) comparing the curves for each sex in Wilson Inlet with that for the corresponding sex in Swan Estuary, using first lengths at age and then back-calculated lengths; and 3) comparing the curves calculated from lengths at age with those obtained from back-calculated lengths, first for males in each system and then for females in each system.

Results

Mean monthly percentages of otoliths from Wilson Inlet with a peripheral translucent zone and one, two, or three inner translucent zones followed similar seasonal trends (Fig. 1). The percentage of such otoliths rose sharply in early spring and fell to close to zero in the late spring or early summer where they

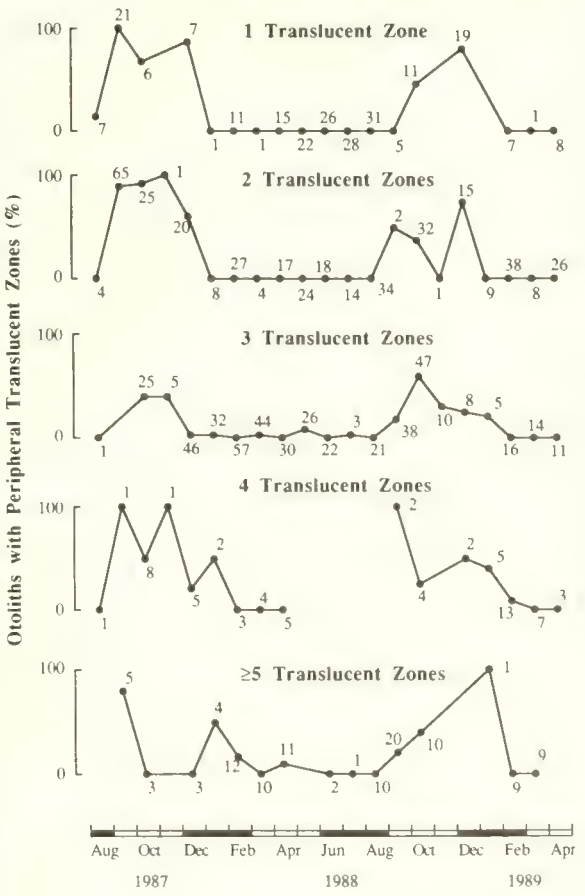

Figure 1

The percentage of lapilli of the eel tailed catfish *Cnidoglanis macrocephalus* from Wilson Inlet possessing a clearly defined peripheral translucent zone in each month. Data are presented separately for otoliths in which there are one to five or more inner translucent zones. Black rectangles on the x-axis represent summer and winter months, white rectangles the autumn and spring months.

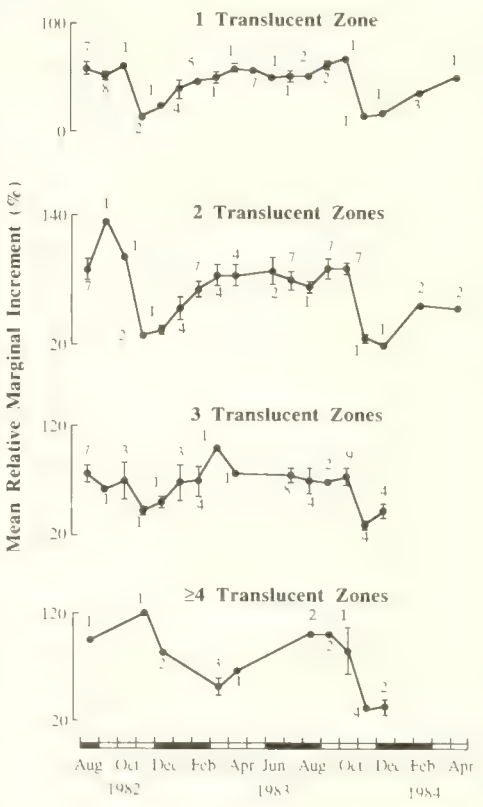

Figure 2

Mean relative marginal increments for asterisci otoliths of the eel tailed catfish, *Cnidoglanis macrocephalus* from the Swan Estuary. Recalculated from the data used by Nel et al. (1985). Data are presented separately for otoliths in which there are one to four or more translucent zones. Standard errors are given when sample size was ≥3. Black rectangles on the x-axis represent summer and winter months, white rectangles the autumn and spring months.

remained through the following summer, autumn, and winter months. Although data for otoliths with both four and five or more translucent zones were less abundant, they followed a similar trend (Fig. 1). The mean marginal increment on otoliths with one, two, and three translucent zones from Swan Estuary fell to a minimum in the spring and rose progressively during the ensuing summer and early autumn, before levelling off in the late autumn and winter (Fig. 2). While the number of otoliths with four or more translucent zones was small, the trend shown by the marginal increment on these otoliths is similar.

A cubic polynomial equation, using logarithm (natural) transformed data, provided the best description of the relationship between otolith radius and total fish length in both Wilson Inlet and Swan Estuary, when lapilli and asterisci otoliths were used, respectively (Fig. 3).

The equations were as follows:

Wilson Inlet

Males: $y = 5.700 + 1.388x - 0.191x^2 - 0.315x^3$ ($R^2 = 0.935$, $P < 0.001$, $n = 462$)

Females: $y = 5.708 + 1.374x - 0.235x^2 - 0.317x^3$ ($R^2 = 0.926$, $P < 0.001$, $n = 876$)

Swan Estuary

Males: $y = 6.152 + 0.951x - 0.875x^2 - 0.400x^3$ ($R^2 = 0.931$, $P < 0.001$, $n = 499$)

Females: $y = 6.174 + 1.171x - 0.479x^2 - 0.230x^3$ ($R^2 = 0.931$, $P < 0.001$, $n = 568$)

Examination of the otoliths suggests that the curvilinearity at the upper end of these relationships (Fig. 3) is due to the otoliths of larger fish tending to thicken rather than lengthen.

The lengths of fish of a given age class were highly variable (Figs 4 and 5). For example, the lengths of female fish that were about four years old in Wilson Inlet ranged from 478 to 631 mm and those that were about three years old in the Swan Estuary ranged from 351 to 591 mm. The predicted lengths of fish, derived from generalized growth curves, were greater when lengths at age rather than back-calculated lengths were used for fish of ages 1 and 2 (Table 1). The high values for R^2 for the generalized growth curves, derived from both lengths at age and back-calculated lengths, show that these curves fit the data well (Table 2). The oldest male and female *C. macrocephalus* caught in Wilson Inlet were $12^3/_4$ years old (718 mm, 1885 g) and $9^3/_4$ years old (670 mm, 1738 g), respectively. The corresponding values for fish from the Swan Estuary were 5 years (582 mm, 1142 g) and $6^3/_4$ years (683 mm, 1880 g), respectively.

The use of common curves in the cases of both lengths at age and back-calculated lengths for each of the two sexes in each system accounted for 89 to 94% of the observed variance. By assuming that a difference exists between the growth curves of the two sexes in each system and with each of the two methods, the fit was improved by only 0.003% for back calculated data for the Swan Estuary and 0.3% for length at age data for Wilson Inlet.

Applying likelihood ratio tests, the length-at-age growth curves for males and females differed significantly in both the Wilson Inlet ($P<0.001$) and Swan Estuary populations ($P<0.05$). Back-calculated growth curves calculated for the two sexes also differed significantly ($P<0.001$) in Wilson Inlet but not in Swan Estuary.

The use of a common curve for each sex by using both lengths at age and back-calculated lengths for

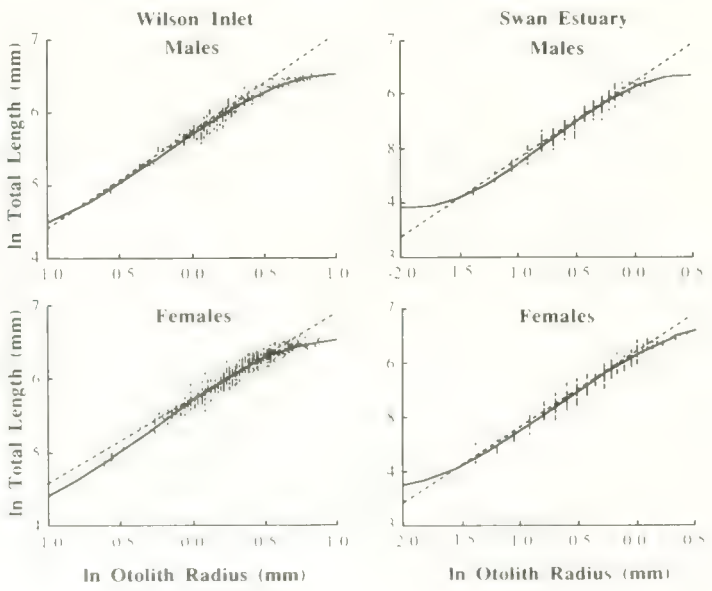

Figure 3

Relationships between the natural logarithms of total length (x) and lapilli radius (y) of the eel tailed catfish *Cnidoglanis macrocephalus* from Wilson Inlet and the Swan Estuary. Broken lines represent the best fit for a linear regression, the solid lines the best fit for the cubic polynomial equation.

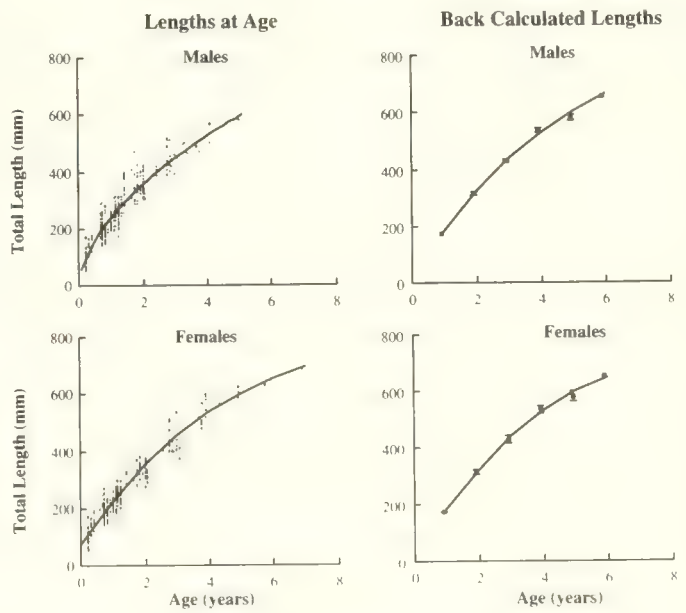

Figure 4

Growth curves obtained from lengths at age and back-calculated lengths of the eel tailed catfish *Cnidoglanis macrocephalus* from Wilson Inlet with the method of Schnute (1981). Mean ±1 standard error of the mean of back-calculated lengths at each age are given.

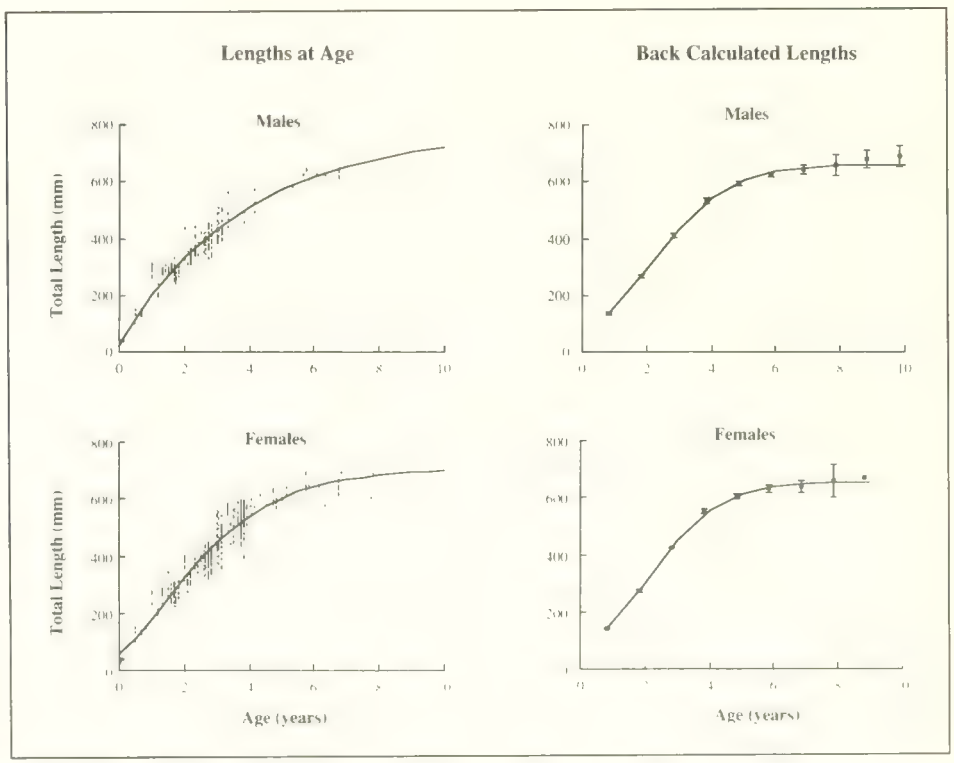

Figure 5

Growth curves obtained from lengths at age and back-calculated length data for the eel tailed catfish *Cnidoglanis macrocephalus* from the Swan Estuary with the method of Schnute (1981). Mean ±1 standard error of the mean of back-calculated lengths at each age are given.

Table 1

The total lengths (mm) at sequential ages of the eel tailed catfish *Cnidoglanis macrocephalos* in Wilson Inlet and Swan Estuary, predicted from generalized growth curves (Schnute, 1981) calculated from lengths at age (LAA) and back-calculated lengths (BCL).

	Wilson Inlet				Swan Estuary			
Age	Male LAA	Female LAA	Male BCL	Female BCL	Male LAA	Female LAA	Male BCL	Female BCL
1	203	180	156	158	239	225	185	184
2	335	324	293	298	356	353	324	323
3	436	449	436	448	447	456	436	440
4	513	541	543	556	525	538	527	531
5	573	603	605	613	594	603	601	598
6	619	643	636	638		654		647
7	655	668	650	648		694		
8	682	684	657	652				
9	703	693	660	653				
10	720	699	661					

Table 2

The parameters of the generalized growth curves fitted to lengths at age and back-calculated lengths for the eel tailed catfish *Cnidoglanis macrocephalus* in Wilson Inlet and Swan Estuary. y_1 and y_2 are lengths (mm) at reference ages 1 and 4 and a and b are the parameters of the growth equation.

Location			y_1	y_2	a	b	R^2	n
Wilson Inlet	Lengths at age	Female	180	541	0.51	0.20	0.90	916
		Male	203	513	0.26	1.04	0.92	502
	Back-calculated lengths	Female	158	556	0.96	−0.99	0.94	2354
		Male	156	543	0.82	−0.71	0.96	1102
Swan Estuary	Length at age	Female	225	537	0.25	0.90	0.91	517
		Male	239	525	0.02	1.75	0.85	447
	Back-calculated lengths	Female	183	530	0.37	0.53	0.90	615
		Male	184	527	0.20	1.04	0.85	426

the populations in the two systems accounted for 90 to 94% of the observed variance. The additional variance explained by assuming a difference between the growth curves for each sex in each system improved the fit to the four data sets by 0.3 to 0.6%. The growth curves estimated for males from lengths at age and from back-calculated lengths in Wilson Inlet differed significantly from those estimated for males in Swan Estuary using the corresponding types of data; the same was true for females ($P<0.001$).

The percentage of the variance explained by the common curves derived from lengths at age and back-calculated lengths for each sex in each system ranged from 81% for males in the Swan Estuary to 94% for both males and females in Wilson Inlet. The percentage of the variance explained by assuming that the growth curves determined from lengths at age and back-calculated lengths are different was improved by 0.8 and 0.2% respectively for males and females from Wilson Inlet and by 4.2 and 1.6% respectively for males and females from the Swan Estuary. The length at age and back-calculated growth curves for males in Wilson Inlet and Swan Estuary differed significantly; the same applied for females ($P<0.001$).

Discussion

The present study of the lapilli of *C. macrocephalus* in Wilson Inlet is the first to demonstrate in a plotosid that each of the otolith's first four translucent zones, and probably all other translucent zones, are formed annually. Furthermore, re-analysis of the data of Nel et al. (1985) has shown that this also applies to the

asterisci in *C. macrocephalus* from the Swan Estuary. The importance of confirming that each successive translucent zone is formed annually is demonstrated by the results obtained by Hyndes et al. (1992) for whole sagittae of *Platycephalus speculator* in Wilson Inlet. In that species, mean monthly marginal increments showed a very clear seasonal trend when individual marginal increments on all unsectioned otoliths were pooled, irrespective of the number of translucent zones. However, they did not show conspicuous trends when the data for the marginal increments on unsectioned otoliths with two, three, four, and five or more translucent zones were each plotted separately. In other words, when marginal increment data for all otoliths were pooled, the pronounced seasonality exhibited by the mean marginal increments on otoliths with one translucent zone of *P. speculator* had an overwhelming influence on the data set.

The von Bertalanffy growth curve did not sufficiently describe the growth of *C. macrocephalus* from Wilson Inlet; the lengths were consistently greater than the mean length at ages 7 and above and showed increasing divergence with age. This was far less of a problem in Swan Estuary where older fish were less abundant. The generalized growth curve provided better fits to the data than the von Bertanlanffy curve for males and females in both systems, when both lengths at age and back-calculated lengths were used. Furthermore, likelihood ratio tests showed that this improvement was significant in three of the four cases for the population in Wilson Inlet. Such improvement is consistent with the observation that when there is an acceleration of growth early in life, the von Bertalanffy growth curve does not provide as adequate a fit as the Schnute, Gompertz, or Richard's curves (Schnute, 1981; Campana and Jones, 1992).

While the presence among younger fish of smaller back-calculated lengths than mean lengths at age (Table 1) would be consistent with Lee's phenomenon (Ricker, 1975), it could also have been brought about by the low numbers of younger fish in the samples. The fits of the common curves constructed for each sex in Wilson Inlet from lengths at age and back-calculated lengths were improved by only 0.2% for females and 0.8% for males when separate curves were used. However, this was not the case for fish in the Swan Estuary, where the sum of squares was improved by 1.6% for females and by as much as 4.2% for the males. The differences in improvement in fit in the two systems probably reflects the fact that, while the 0+ age class in the Swan Estuary was caught in greater numbers, it tended to be represented in samples by the larger members of this age class.

The improvement of fit obtained by using separate growth curves was small, both in comparisons between males and females in Wilson Inlet and Swan Estuary and in comparisons between corresponding sexes in the two systems. This applied to curves constructed both from lengths at age and back-calculated lengths. In none of these cases was the sum of squares improved by more than 0.6%. However, although the differences between the curves for each sex in each system and for the corresponding sexes in the two populations were small, and even though the lengths varied considerably at a given age, the curves were still statistically different with a likelihood ratio test (usually $P<0.001$). These differences probably reflect the influence of the large number of data points used to construct the growth curves.

The small magnitude of the differences between these growth curves is demonstrated by the fact that at age 4, the lengths of males and females in Wilson Inlet and the Swan Estuary, predicted from the generalized growth curve, generally differed by less than 3%, irrespective of whether the curve was constructed from lengths at age or back-calculated lengths. Thus, although there were usually highly statistically significant differences between curves, the actual differences between the curves for the two sexes in each population and between the corresponding sexes in those populations are almost certainly of limited biological significance.

In conclusion, the growth of *C. macrocephalus* in Wilson Inlet was similar to that in the Swan Estuary. This similarity occurred despite the fact that water temperatures in the latter system were over 5°C higher in the summer (c.f. Loneragan and Potter, 1990; Potter et al., 1993). Wilson Inlet is eutrophic and therefore more productive (Lukatelich et al., 1987) and consequently contains a greater abundance of the large deposit-feeding benthic invertebrates[1] that make a major contribution to the diet of *C. macrocephalus* (Nel et al., 1985; Laurenson, 1992). Therefore the similarity between the growth rate of *C. macrocephalus* in Wilson Inlet and the Swan Estuary may reflect a compensation for lower water temperatures by greater prey abundance.

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[1] Platell, M. School of Biological and Environmental Sciences, Murdoch Univ., Murdoch, Western Australia 6150, Australia. Personal commun., 1991.

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Literature cited

Ayvazian, D. G., M. S. Johnson, and D. J. McGlashan.
1994. High levels of genetic subdivision of marine and estuarine populations of the estuarine catfish *Cnidoglanis macrocephalus* (Plotosidae) in southwestern Australia. Mar. Biol. 118:25–31.

Beamish, R. J., and G. A. McFarlane.
1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735–743.

Beckman, D. W., C. A. Wilson, and A. L. Stanley.
1989. Age and growth of red drum, *Sciaenops ocellatus*, from offshore waters of the northern Gulf of Mexico. Fish. Bull. 87:17–27.

Beckman, D. W., A. L. Stanley, J. H. Render, and C. A. Wilson.
1990. Age and growth of black drum in Louisiana waters of the Gulf of Mexico. Trans. Am. Fish. Soc. 119:537–544.

Buxton, C. D.
1993. Life-history changes in exploited reef fishes on the east coast of South Africa. Environ. Biol. Fishes 36:47–63.

Campana, S. E., and C. M. Jones.
1992. Analysis of otolith microstructure data. *In* D. K. Stevenson and S. E. Campana (eds.), Otolith microstructure examination and analysis. Can. J. Fish. Aquat. Sci. 117:73–100.

Casselman, J. M.
1987. Determination of age and growth. *In* A. H. Weatherley and H. S. Gill (eds.), The biology of fish growth, p.209–242. Academic Press, London.

Cerrato, R. M.
1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Can. J. Fish. Aquat. Sci. 47:1416–1426.

Collins, M. E., D. J. Schmidt, W. C. Waltz, and J. L. Pickney.
1989. Age and growth of king mackerel, *Scomberomorus cavalla*, from the Atlantic coast of the United States. Fish. Bull. 87:49–61.

Crozier, W. W.
1989. Age and growth of angler-fish *Lophius piscatorius* L. in the north Irish Sea. Fish. Res. (Amst.) 7:267–278.

Francis, R. I. C. C.
1990. Back calculations of fish lengths: a critical review. J. Fish. Biol. 36:883–902.

Hampton, J.
1991. Estimation of southern bluefin tuna *Thunnus maccoyii* growth parameters from tagging data, using von Bertalanffy models incorporating individual variation. Fish. Bull. 89:577–590.

Hoese, D. F., and J. E. Hanley.
1989. Plotosidae. *In* J. R. Paxton, D. F. Hoese, G. R. Allen, and J. E. Hanley (eds.), Zoological catalogue of Australia. Vol 7: Pisces: Petromyzontidae to Carangidae, p. 222–226. Australian Government Publishing Service, Canberra.

Hutchins, B., and R. Swainston.
1986. Sea fishes of southern Australia. Swainston Publishing, Perth.

Hyndes, G. A., N. R. Loneragan, and I. C. Potter.
1992. Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead, *Platycephalus speculator*. Fish. Bull. 90:276–284.

Ihnen, L.A., and J.H. Goodnight.
1987. The NLIN procedure. *In* R. C. Luginbuhl, S. D. Scholtzhauer, J. C. Parker and K. P. Ingraham (eds.), SAS/STAT guides for personal computers, Version 6 ed. SAS Institute, Cary, North Carolina.

Kimura, D. K.
1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77:765–776.

Kirkwood, G. P.
1983. Estimation of von Bertalanffy growth curve parameters using length increment and age-length data. Can. J. Fish. Aquat. Sci. 40:1405–1411.

Kowarsky, J.
1976. Clarification of the name and distribution of the plotosid catfish *Cnidoglanis macrocephalus*. Copeia 1976:593–594.

Laurenson, L. J. B.
1992. Biology and commercial exploitation of the estuarine catfish, *Cnidoglanis macrocephalus* (Valenciennes), in south western Australia with emphasis on the seasonally closed Wilson Inlet. Ph.D. diss., Murdoch Univ., Perth, Western Australia.

Laurenson, L. J. B., F. J. Neira, and I. C. Potter.
1993a. Reproductive biology and larval morphology of the marine plotosid *Cnidoglanis macrocephalus* (Teleostei) in a seasonally closed Australian estuary. Hydrobiologia 268:179–192.

Laurenson, L. J. B., I. C. Potter, R. C. J. Lenanton, and N. G. Hall.
1993b. The significance of size at sexual maturity, mesh size and closed fishing waters to the commercial fishery for the catfish *Cnidoglanis macrocephalus* in Australian estuaries. J. Appl. Ichthyol. 9:210–221.

Lenanton, R. C. J., and I. C. Potter.
1987. Contribution of estuaries to commercial fisheries in temperate Western Australia and the concept of estuarine dependence. Estuaries 10:28–35.

Loneragan, N. R., and I. C. Potter.
1990. Factors influencing community structure and

distribution of different life-cycle categories of fishes in shallow waters of a large Australian estuary. Mar. Biol. (Berl.) 106:25–37.

Loneragan, N. R., I. C. Potter, and R. C. J. Lenanton.
1989. Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary. Mar. Biol. (Berl.) 103:461–479.

Lukatelich, R. J., N. J. Schofield, and A. J. McComb.
1987. Nutrient loading and macrophyte growth in Wilson Inlet, a bar-built southwestern Australian estuary. Estuarine Coastal Shelf Sci. 24:141–165.

Maceina, M. J., D. N. Hata, T. L. Linton, and A. M. Landrey Jr.
1987. Age and growth analysis of spotted sea trout from Galveston Bay, Texas. Trans. Am. Fish. Soc. 116:54–59.

Neira, F. J., and I. C. Potter.
1992. The ichthyoplankton of a seasonally closed estuary in temperate Australia. Does an extended period of opening influence species composition? J. Fish Biol. 41:935–953.

Nel, S. A., I. C. Potter, and N. R. Loneragan.
1985. The biology of the catfish *Cnidoglanis macrocephalus* (Plotosidae) in an Australian estuary. Estuarine Coastal Shelf Sci. 21:895–909.

Potter, I. C., G. A. Hyndes, and F. M. Baronie.
1993. The fish fauna of a seasonally closed Australian estuary. Is the prevalence of estuarine-spawning species high? Mar. Biol. (Berl.) 116:19–30.

Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.

Schnute, J.
1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38:1128–1140.

A comparison of larval and postlarval gulf menhaden, *Brevoortia patronus*, growth rates between an offshore spawning ground and an estuarine nursery

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The fishery for gulf menhaden, *Brevoortia patronus*, was the largest by weight in the United States from 1963 through 1988 and has had a significant impact on the economy of the northern Gulf of Mexico coast. The species is also an ecologically important prey item for a number of commercially and recreationally important species (Lassuy, 1983).

Gulf menhaden early life history has been reviewed by a number of authors (Lassuy, 1983; Deegan, 1985; Powell and Phonlor, 1986; Shaw et al., 1988; Christmas and Waller[1]). Adults spawn in offshore and coastal waters in depths ranging from 11 to 128 m; peak spawning occurs between the 10- and 60-m isobaths (Shaw et al., 1988). Most spawning generally occurs between October and March; peak spawning occurs in December (Fore, 1970; Shaw et al., 1985; Christmas and Waller[1]). Once spawned, gulf menhaden eggs are pelagic and hatch within about two days. The offshore larval drift period may last from 4 to 10 weeks (Deegan and Thompson, 1987; Shaw et al., 1988). Peak immigration through tidal passes into estuarine nurseries generally occurs between December and March (Suttkus, 1956; Lassuy, 1983).

In the estuary, larval gulf menhaden move into bayous and other low salinity areas at the onset of transformation into juveniles (Fore and Baxter, 1972; Simoneaux, 1979; Deegan, 1990; Raynie and Shaw, in press). Estuarine residence is typical during summer months. As juveniles grow larger, they tend to move downstream to higher salinity waters and from late summer to winter many emigrate to open coastal waters (Deegan, 1990).

Daily otolith increment formation has been validated and is estimated to begin at the onset of exogenous feeding, which occurs about three days after hatching (Warlen, 1988). Growth rate estimates based on larval gulf menhaden otolith analyses have been made from larvae collected off the Mississippi River Delta, Florida and Texas (Warlen, 1988) and from young of the year collected within estuarine waters of Louisiana (Deegan and Thompson, 1987). A comparison between growth rates of gulf menhaden captured from continental shelf and adjacent estuarine waters during the same time period has not been done. The purpose of this paper is to examine growth rates of larval and postlarval gulf menhaden from offshore and estuarine habitats and relate the results to metamorphosis.

Materials and methods

Sampling procedure

Gulf menhaden larvae and postlarvae were collected at two stations in the northern Gulf of Mexico (6 and 32 km from shore) on 23 January 1990 and from three locations (Lower Bay, Mosquito Island, and Big Carencro Bayou) within the adjacent estuary, Fourleague Bay, Louisiana, on 24–25 January 1990 (see Raynie and Shaw, in press). Larvae were collected offshore with a 60-cm bongo frame equipped with a 505-µm mesh net fitted with a flow meter (General Oceanics Model no. 2030). Within Fourleague Bay, collections were made with a bow-mounted plankton push net of the same diameter and mesh size as that used offshore. One three-minute collection was taken at each station offshore and at each station each day within Fourleague Bay. Plankton push nets have been shown to be effective at collecting larval fish (Miller, 1973; Raynie and Shaw, in press) and juvenile fish (Herke, 1969; Kriete and Loesch, 1980). The use of this gear in this highly turbid and shallow estuarine system (mean depth=1.5 m; Teague et al., 1988) minimizes net avoidance.

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[1] Christmas, J. Y., and R. S. Waller. 1975. Location and time of menhaden spawning in the Gulf of Mexico. CCRL/NMFS Contract Rep. 03-4-042-24.

Manuscript accepted 16 March 1994.
Fishery Bulletin 92:890–894.

Samples were initially preserved with 95% ethanol, stored in ice, and later preserved with a 70% ethanol solution in the lab. Temperature and salinity were measured with a Beckman Portable Electronic Salinometer (Model No. RS5-3).

Laboratory analysis

Notochord lengths (preflexion, NL) or standard lengths (SL) were measured to the nearest 0.1 mm with an ocular micrometer under a dissecting microscope. Sagittal otoliths were then removed from a random subsample (n=111) of larvae under a dissecting microscope with polarized light. Otoliths were air-dried and mounted on a glass microscope slide with S/P Accu-mount 60. Otoliths were sufficiently thin and rings sufficiently spaced to allow for optical sectioning (focusing to the plane of maximum clarity) under a compound microscope (400× or 1,000×) to make total increment counts and otolith diameter measurements. Increments were independently counted by each author and averaged.

Spawning dates were back-calculated for each larva by subtracting the estimated age from date of capture (i.e. capture date – [ring count + 5 days for egg incubation and yolk-sac absorption]) (Warlen, 1988). It was assumed that there were no differences in the age at first increment deposition (5 days) among larvae.

Statistical analysis

Age and growth data from each environment (offshore and estuarine) and the combined data were fit to the Laird version of the Gompertz growth equation (Laird et al., 1965) by means of nonlinear least squares regression techniques (SAS Institute, Inc., 1985):

$$L_t = L_0 e^{K\{1 - e^{-at}\}},$$

where L_t = standard length of larvae at day t ; L_0 = initial length; $K = A_0/a$; A_0 = age-specific growth rate at L_0; and a = the exponential decline in the age-specific growth rate. Because five days were added to otolith counts to attain age estimates (2 days incubation + 3 days between hatching and exogenous feeding and first increment formation), two days were subtracted from the age estimates, so that the Y-intercept would approximate the hatching length. The length at hatching has been observed from laboratory data (2.6–3.0 mm NL; Hettler, 1984) and estimated from field data (2.4 mm NL; Warlen, 1988). With these data, we fixed the hatching length at 3.0 mm NL in our models.

Average daily growth rate was estimated by

$$\text{Average daily growth} = \frac{(\text{standard length} - 3.0\ \text{mm})}{\text{days posthatch}}$$

(after Deegan and Thompson, 1987).

Results and discussion

The mean surface water temperature offshore at the time of capture was 17.8°C (range 17.5–18.0°C) and the mean salinity was 31.0 ppt (range 29.0–33.0 ppt). Within Fourleague Bay, the mean temperature was 19.0°C (range 17.5–20.1°C) and salinities ranged from 2.7 to 7.3 ppt, with the exception of our 24 January 1990 Lower Bay collection when the salinity was 23.9 ppt.

According to age estimates, most of the larvae collected offshore were spawned within one week between 27 December 1989 and 3 January 1990. Virtually all larvae collected within Fourleague Bay were spawned between mid-November and 24 December 1989, with a peak between 17 and 24 December 1989 (Fig. 1). One 85-day-old larva was col-

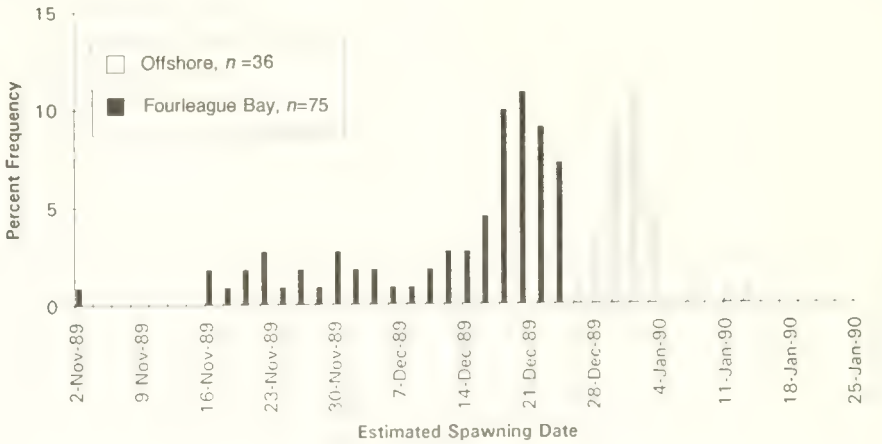

Figure 1

Percent frequency of birth (spawning) dates estimated from otolith increment data for gulf menhaden collected offshore and within Fourleague Bay, Louisiana, between 23 and 25 January 1990. n=number of larvae collected from each environment.

lected from Mosquito Island and was estimated to have been spawned on 1 November 1989.

Growth of larval fish (and other vertebrates) typically proceeds through a series of consecutive intervals (thresholds) which characterize ontogeny. Periods of rapid growth are generally followed by periods of slower development during which complex structures prepare for the next series of changes (Balon, 1984). The Laird-Gompertz equation has been used to describe larval fish growth when the length-age plots are nonlinear and upper asymptotes are apparent (Zweifel and Lasker, 1976; Methot and Kramer, 1979; Laroche et al., 1982; Warlen and Chester, 1985; Warlen, 1988). This model was used to estimate the age-specific growth rate and the exponential decline in the age-specific growth rate as larval gulf menhaden approach metamorphosis to juveniles.

Growth rates were estimated from larvae between 5.8 and 16 mm SL collected offshore and larvae between 17 and 24 mm SL collected within Fourleague Bay. The average daily growth of larvae collected offshore (0.44 mm/day) was greater than within Fourleague Bay (0.12 mm/day). The average daily growth rate of larval gulf menhaden from the combined data was 0.25 mm/day.

Postlarval gulf menhaden are estimated to be 15–25 mm SL (Shaw et al., 1988) upon entering the estuary and begin transformation to the juvenile stage around 20 mm SL. Transformation is complete at about 30 mm (Suttkus, 1956; Hettler, 1984). Between 20 and 30 mm SL, however, growth characteristics change (Fig. 2): mouth parts and gill rakers are modified and the body begins to thicken and take on the deep-bodied characteristics of juveniles and adults (Suttkus, 1956). During this threshold, postlarval (prejuvenile) gulf menhaden growth in weight is disproportionately greater than growth in length (Deegan and Thompson, 1987).

The period of slowed growth in length just before and during juvenile transformation is followed by a dramatic increase in growth rate (Springer and Woodburn, 1960; Deegan and Thompson, 1987). Average daily growth of gulf menhaden between 18 and 82 mm SL reportedly ranges from 0.20 to 0.48 mm/day within Fourleague Bay (Deegan and Thompson, 1987). Our estimate of average daily growth rate for postlarvae (17–24 mm SL) within Fourleague Bay was expectedly lower (0.12 mm/day), since our larvae were approaching or were in the process of transformation.

Our estimate of average daily growth from offshore is similar to Warlen's (1988) growth estimates for larval gulf menhaden collected off Southwest Pass, Louisiana (0.28–0.42 mm/day). Some marine larvae have been shown to grow faster at higher temperatures (Laurence et al., 1981); however, this has not been demonstrated for gulf menhaden (Warlen, 1988). During the winter, surface water temperatures are generally warmer offshore than within Fourleague Bay; however, this difference is generally minimal (Raynie and Shaw, in press). Our temperature data are insufficient (and may be atypical of the average conditions) to evaluate the relationship between growth and temperature. The difference in growth rates between environments, however, is most likely the result of ontogeny. A 71% decrease in growth rate between larval and juvenile

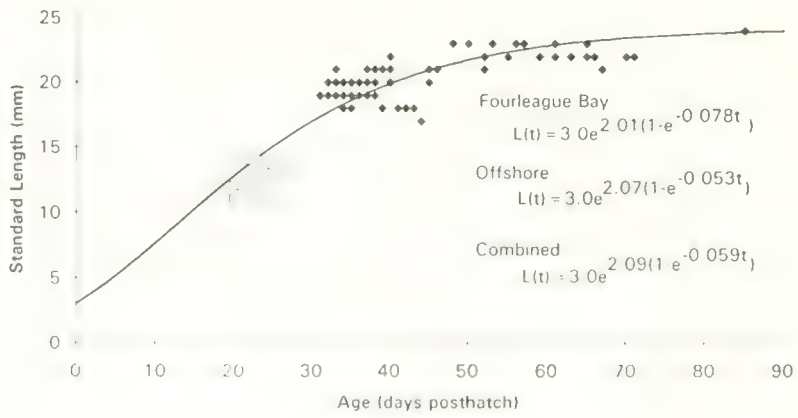

Figure 2

Laird-Gompertz growth models for larval gulf menhaden collected from offshore (n=36) and Fourleague Bay (n=75), Louisiana, between 23 and 25 January 1990. n=number of larvae from each environment.

stages based on developmental history alone has been shown for Atlantic herring, *Clupea harengus*, and a 96% decrease in growth rate has been shown for bay anchovy, *Anchoa mitchilli* (Houde, 1987). These two clupeiform species have high larval growth rates and relatively long metamorphosis intervals (Houde, 1987) as does gulf menhaden. Lewis et al. (1972) also related varying growth in length to growth in weight through larval, prejuvenile, and juvenile stages of Atlantic menhaden, *Brevoortia tyrannus*. Therefore, physiological and morphological changes occurring between larval and juvenile stages may be more important in the regulation of the shape of growth curves (both length and weight) than variability in exogenous factors.

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Literature cited

Balon, E. K.
1984. Reflections on some decisive events in the early life of fishes. Trans. Am. Fish. Soc. 113:178–185.

Deegan, L. A.
1985. The population ecology and nutrient transport of gulf menhaden in Fourleague Bay, Louisiana. Ph.D. diss., Louisiana State Univ., Baton Rouge, 134 p.
1990. Effects of estuarine environmental conditions on population dynamics of young-of-the-year gulf menhaden. Mar. Ecol.-Prog. Ser. 68:195–205.

Deegan, L. A., and B. A. Thompson.
1987. Growth rate and early life history of young-of-the-year gulf menhaden as determined from otoliths. Trans. Am. Fish. Soc. 116:663–667.

Fore, P. L.
1970. Oceanic distribution of the eggs and larvae of the gulf menhaden. *In* Report of the Bureau of Commercial Fisheries Biology Lab, Beaufort, North Carolina, for fiscal year ending June 30, 1968, p. 11–13. U.S. Fish Wildl. Serv. Circ. 341.

Fore, P. L., and K. N. Baxter.
1972. Diel fluctuations in the catch of larval gulf menhaden, *Brevoortia patronus*, at Galveston Entrance, Texas. Trans. Am. Fish. Soc. 101(4):729–732.

Herke, W. H.
1969. A boat-mounted surface push-trawl for sampling juveniles in tidal marshes. Prog. Fish-Cult. 31(3):177–179.

Hettler, W. F.
1984. Description of eggs, larvae, and early juveniles of gulf menhaden, *Brevoortia patronus*, and comparisons with Atlantic menhaden, *B. tyrannus*, and yellowfin menhaden, *B. smithi*. Fish. Bull. 82:85–95.

Houde, E. D.
1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2:17–29.

Kriete, W. H., Jr., and J. G. Loesch.
1980. Design and relative efficiency of a bow-mounted pushnet for sampling juvenile pelagic fishes. Trans. Am. Fish. Soc. 109:649–652.

Laird, A. K., S. A. Tyler, and A. D. Barton.
1965. Dynamics of normal growth. Growth 29:233–248.

Laroche, J. L., S. L. Richardson, and A. A. Rosenberg.
1982. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. Fish. Bull. 80:93–104.

Lassuy, D. R.
1983. Species profiles: life histories and environmental requirements (Gulf of Mexico)—gulf menhaden. U.S. Fish and Wildl. Serv., Div. Biol. Serv. FWS/OBS-82/11.2 and U.S. Army Corps of Engineers, TR EL-82-4, 13 p.

Laurence, C. G., A. S. Smigielski, T. A. Halavik, and B. R. Burns.
1981. Implications of direct competition between larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in laboratory growth and survival studies at different food densities. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:304–311.

Lewis, R. M., E. P. H. Wilkens, and H. R. Gordy.
1972. A description of young Atlantic menhaden, *Brevoortia tyrannus*, in the White Oak River estuary, North Carolina. Fish. Bull. 70:115–118.

Methot, R. D., Jr., and D. Kramer.
1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull. 77:413–423.

Miller, J. M.
1973. A quantitative push-net system for transect studies of larval fish and macrozooplankton. Limnol. Oceanogr. 18(1):175–178.

Powell, A. B., and G. Phonlor.
1986. Early life history of Atlantic menhaden, *Brevoortia tyrannus*, and gulf menhaden, *B. patronus*. Fish. Bull. 84:991–994.

Raynie, R. C., and R. F. Shaw.
In press. Ichthyoplankton abundance along a recruitment corridor from offshore spawning to es-

tuarine nursery ground. Estuarine Coastal Shelf Sci.

SAS Institute, Inc.
1985. SAS user's guide: statistics, 1985 ed. Cary, NC, SAS Institute Inc., 584 p.

Shaw, R. F., B. D. Rogers, J. H. Cowan Jr., and T. L. Tillman.
1985. Distribution and density of *Brevoortia patronus* (gulf menhaden) eggs and larvae in the continental shelf off western Louisiana. Bull. Mar. Sci. 36:96–103.

Shaw, R. F., B. D. Rogers, J. H. Cowan Jr., and W. H. Herke.
1988. Ocean-estuarine coupling of ichthyoplankton and nekton in the northern Gulf of Mexico. Am. Fish. Soc. Symp. 3:77–89.

Simoneaux, L. F.
1979. The distribution of menhaden, genus *Brevoortia*, with respect to salinity, in the upper drainage basin of Barataria Bay, Louisiana. M.S. thesis, Louisiana State Univ., Baton Rouge, 96 p.

Springer, V. G., and K. D. Woodburn.
1960. An ecological study of the fishes of the Tampa Bay area. Florida Board of Conservation Marine Laboratory Professional Paper Series 1, 104 p.

Suttkus, R. D.
1956. Early life history of the gulf menhaden, *Brevoortia patronus*, in Louisiana. Trans. N. Am. Wildl. Conf. 21:390–407.

Teague, K. G., C. J. Madden, and J. W. Day Jr.
1988. Sediment-water oxygen and nutrient fluxes in a river-dominated estuary. Estuaries 11:1–9.

Warlen, S. M.
1988. Age and growth of larval gulf menhaden, *Brevoortia patronus*, in the northern Gulf of Mexico. Fish. Bull. 86:77–90.

Warlen, S. M., and A. J. Chester.
1985. Age, growth, and distribution of larval spot, *Leiostomus xanthurus*, off North Carolina. Fish. Bull. 83:587–599.

Zweifel, J. R., and R. Lasker.
1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull. 74:609–621.

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Errata

Erratum: Fish. Bull. 91:310–327.

Prager, M. H., and A. D. MacCall. 1993.
Detection of contaminant and climate effects on spawning success of three pelagic fish stocks off southern California: Northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and chub mackerel *scomber japonicus*.

Correction: On page 319, in Table 5, the R^2 statistic for the "combined" model of Pacific sardine is given as 0.47. The correct figure is 0.83, as stated on page 322.

Erratum: Fish. Bull. 92:374–389.

Prager, M. H. 1994.
A suite of extensions to a nonequilibrium surplus-production model.

Correction: On page 376, in Equation 8a, a term containing "–1" was misplaced. The correct equation is

$$F_\tau = \frac{\beta Y_\tau}{\ln\left[\frac{\beta B_\tau (e^{\alpha_\tau} - 1)}{\alpha_\tau} + 1\right]}.$$

Publication Awards, 1992

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The Publications Advisory Committee of the National Marine Fisheries Service is pleased to announce the awards for best publications authored by NMFS scientists and published in the Fishery Bulletin for 1992 and in Marine Fisheries Review for 1992. Eligible papers are nominated by the Fisheries Science Centers and Regional Offices and are judged by the NMFS Editorial Board. Only articles that significantly contribute to the understanding and knowledge of NMFS-related studies are eligible. We offer congratulations to the following authors for their outstanding efforts.

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Energetics of associated tunas and dolphins in the eastern tropical Pacific Ocean: a basis for the bond. Fish. Bull. 90:678–690. Elizabeth Edwards is with the Southwest Fisheries Science Center, La Jolla, California.

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Variability in spiny lobster *Panulirus maginatus* recruitment and sea level in the Northwestern Hawaiian Islands. Fish. Bull. 90:483–493. Jeffrey Polovina is with the Southwest Fisheries Science Center, Honolulu, Hawaii.

Marine Fisheries Review, 1992

Outstanding Publication

Robin S. Waples

Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the Endangered Species Act. Mar. Fish. Rev. 53(3)11–22. Robin Waples is with the Northwest Fisheries Science Center, Seattle, Washington.

Honorable Mention

Dean W. Ahrenholz

Population biology and life history of the North American menhadens, *Brevoortia* spp. Mar. Fish. Rev. 53(4):3–19. Dean Ahrenholz is with the Southeast Fisheries Science Center, Beaufort, North Carolina.

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(See instructions on reverse)

PS Form 3526, Feb. 1989

Fishery Bulletin

Guide for Contributors

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Text must be typed double-spaced throughout. A brief introduction should portray the broad significance of the paper; the remainder of the paper should be divided into the following sections: **Materials and methods**, **Results**, **Discussion** (or **Conclusions**), and **Acknowledgments**. Headings within each section must be short, reflect a logical sequence, and follow the rules of multiple subdivision (i.e. there can be no subdivision without at least two items). The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be spelled out the first time they are mentioned. The scientific names of species must be written out the first time they are mentioned; subsequent mention of scientific names may be abbreviated. Follow the *U.S. Government Printing Office Style Manual* (1984 ed.) and the *CBE Style Manual* (5th ed.) for editorial style, and the most current issue of the American Fisheries Society's *Common and Scientific Names of Fishes from the United States and Canada* for fish nomenclature. Dates should be written as follows: 11 November 1991. Measurements should be expressed in metric units, e.g., metric tons as (t); if other units of measurement are used, please make this fact explicit to the reader. The numeral one (1) should be typed as a one, not as a lower-case el (l).

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